Part 2. Systematics of the Bivalvia

lan G. Speden

Bulletin 33

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The Type Fox Hills Formation, Cretaceous (Maestrichtian), South Dakota

Part 2. Systematics of the Bivalvia

IAN G. SPEDEN

Geological Survey of New Zealand Lower Hutt

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ABSTRACT

F. B. Meek's classical studies (1856–1876) on the faunas of the Fox Hills Formation in its type area, north-central South Dakota, provided an important basis for the zonation and correlation of the latest Cretaceous sequences of the Western Interior of the United States. In its type area the Fox Hills fauna is dominated specifically and numerically by bivalves. This publication presents a revision of the Fox Hills Bivalvia, using the concepts of population systematics, undertaken to provide the basis for paleoecological studies.

Approximately 100,000 specimens, over two tons of fossils, from 264 localities were collected for the study, and type and older collections were examined where possible. To aid comparisons detailed species descriptions documented by simple statistical parameters and illustrations are given. Generic diagnoses are emended where necessary, and the generic placement of many species is changed.

Forty-nine bivalve genera are recognized. Two of these are new: Nymphalucina, type species Tellina occidentalis Morton (= Lucina occidentalis), and Sourimis, type species Tellina equilateralis Meek & Hayden. The diagnoses of the following genera are emended or supplemented: Pseudoptera Meek, Clisocolus Gabb, Tellinimera Conrad, and Opertochasma Stephenson. Fifty-eight species, including seven new species, Nuculana (N.) grandensis, Yoldia lacrima, Y. rectangularis, Spaniorinus nicolleti, Hindsiella corsonensis, Cyrtodaria minuta, and Pholadomya deweyensis, are described. The relationship of Modiolus meeki (Evans & Shumard) and M. galpinianus (Evans & Shumard) is clarified, and Syncyclonema halli (Gabb), the type species of the genus, and Tenuipteria fibrosa (Meek & Hayden) are described adequately for the first time.

This study indicates that the status and generic placement of many species described from the Upper Cretaceous of the Western Interior require revision. Some species are probably based on juvenile specimens. Others are defined on inadequate data.

ZUSAMMENFASSUNG

Die klassischen Forschungen von F. B. Meek (1856–1876) mit der Fauna von der Fox Hills Formation in seinem Typlokalität, Nord-zentral South Dakota, geben eine wichtige Basis für die Einteilung und Korrelation von der jungsten Kreide Schichtfolge im westlichen Binnenland der Vereinigten Staaten. In seinem Typlokalität der Fox Hills Fauna ist spezifisch und zahlmässig von Bivalvia beherrscht. Diese Veröffentlichung stellt eine Revision der Fox Hills Bivalvia dar. Die Begriffe der Zahl-Systematik werden gebraucht, um die Grundlage für die paleoecologischen Untersuchungen zu geben.

Ungefähr 100,000 Proben, mehr als zwei Tonnen Fossilen, von 264 Lokalitäten wurden für diese Forschungen gesammelt. Wo möglich wurden Typ und ältere Sammlungen untersucht. Um Vergleichtsmöglichkeiten aufzuführen wur-

den ausführliche Beschreibungen von Arten von einfachen statischen Parametern und Abbildungen vorgelegt. Die generischen Diagnosen wurden, wenn nötig, verbessert und die generische Stellung von viele arten geändert.

Neunundvierzig Gattungen von Bivalvia wurden festgestellt. Zwei von dieser sind neu: Nymphalucina, Typ-Art Tellina occidentalis Morton (= Lucina occidentalis), und Sourimis, Typ-Art Tellina equilateralis Meek & Hayden. Die Diagnose von den folgenden Gattungen sind verbessert oder ergänzt: Pseudoptera Meek, Clisocolus Gabb, Tellinimera Conrad, und Opertochasma Stephenson. Achtundfunfzig Arten, einschliesslich sieben neue Arten, Nuculana (N.) grandensis, Yoldia lacrima, Y. rectangularis, Spaniorinus nicolleti, Hindsiella corsonensis, Cyrtodaria minuta, und Pholadomya deweyensis sind beschrieben. Der Zusammenhang zwischen Modiolus meeki (Evans & Shumard) und M. galpinianus (Evans & Shumard) ist erläutert. Syncyclonema halli (Gabb), die Typ-Art der Gattung, und Tenuipteria fibrosa (Meek & Hayden) werden zum ersten Mal ausreichend beschrieben.

Diese Forschung zeigt, dass der Status und die generische Stellung von vielen beschriebenen Arten aus der Oberkreide des westlichen Binnenlandes nocheinmal überprüft werden sollte. Einige Arten sind wahrscheinlich an jugendliche Proben begrundet. Andere sind an unzureichende Daten bestimmt.

РЕЗЮМЕ

Классические исследования фаун формации Фокс Хиллс в ее типовой области, северной части средней Южной Дакоты, выполнены Ф. Б. Миком (1856-1876), создали важную основу для распределения по зонам и коррелирования позднейших меловых отложений запада внутренней части Соединенных Штатов. В ее типовой области фауна Фокс Хиллс доминирована двустворчатыми моллюсками, как по числу видов, так и по числу индивидуумов. Настоящий доклад является ревивией Вivalvia формации Фокс Хиллс, использующей понятия систематики популяций и сделанной с целью создания основы для палеоэкологических исследований.

Для настоящих исследований собрано около 100 000 экземпляров, больше двух тон фоссилов из 264 местностей, а типовые и другие старшие коллекции исследованы когда это было возможно. Для облегчения сравнений даны подробные описания видов, документированные простыми статистическими параметрами и иллюстрациями. Диагнозы родов исправлены когда это было необходимо и ро-

довые положения многих видов изменены.

Признаются сорок девять родов двустворчатых. Два из этих родов — новые: Nymphalucina, с тиновым видом Tellina occidentalis Morton (= Lucina occidentalis) и Sourimis, с тиновым видом Tellina equilateralis Meek & Hayden. Изменены или дополнены диагнозы следующих родов: Pseudoptera Meek, Clisocolus Gabb, Tellinimera Conrad и Opertochasma Stephenson. Описаны пятьдесят восемь видов, включая семь новых: Nuculana (N.) grandensis, Yoldia lacrima, Y. rectangularis, Spaniorinus nicolleti, Hindsiella corsonensis, Cyrtodaria minuta и Pholadomya deweyensis. Разъяснено взаимоотношение Modiolus meeki (Evans & Shumard) и М. galpinianus (Evans & Shumard). Syncyclonema halli (Gabb), типовой вид его рода, а тоже Tenuipteria fibrosa (Meek & Hayden) описаны удовлетворительно в первый раз.

Настоящее исследование показывает, что статус и родовое положение многих видов из верхнего мела запада внутренней части Соединенных Штатов требуют ревизии. Некоторые из этих видов, вероятно, основываются на юных экземплярах,

другие определены на основании недостаточных данных.

INTRODUCTION

The abundance, diversity and excellent preservation of fossils in the Fox Hills Formation of the Missouri River region were noted over a century ago by Meek and Hayden (1856a, b, c). They (1856c) also stressed the dominance of the faunas by bivalves and other molluscs. Meek and Hayden's observations were confirmed by Waage (1961) during his initial investigations of the Fox Hills Formation, which outcrops immediately west of the Missouri River in Corson, Dewey and eastern Ziebach counties, north-central South Dakota (Fig. 1). Waage's study showed that the formation undergoes rapid but gradational lateral and vertical lithofacies changes related to deposition along the margin of the regressing Upper Cretaceous (Maestrichtian) sea of the Western Interior. The study also indicated the existence of distinctive stratigraphic and geographic faunal patterns, including changes in faunal composition and taxonomic dominance.

The availability of a detailed stratigraphic framework in a structurally uncomplicated flat-lying sequence (Figs. 2, 3; Waage, 1961, 1968) and the abundance of well-preserved fossils that have undergone minimal transportation offer an ideal setting for a paleozoological study emphasizing the patterns of species distributions and the factors controlling these distributions. An additional advantage of the dominance of the fauna by bivalves is that, largely through the work of C. M. Yonge and his associates, the class is ecologically and functionally the best understood of any molluscan group.

Two related studies were made of the Fox Hills bivalves:

1) Revision of the systematics of the 58 species comprising the bivalve fauna; published herein. 2) Paleozoological interpretation of the species, of the associations of species in assemblages, and of the faunas of the biostratigraphic units. This will be published elsewhere.

Systematics is an essential prerequisite to comprehensive paleobiological studies and provides a basis for paleoecological interpretations. Paleoecological interpretations are in turn dependent on the stratigraphic framework, on the empirical patterns shown by fossil species in the stratigraphic framework, and on a detailed knowledge of living organisms (Speden, 1966). As a century has elapsed since Meek and Hayden's monumental work it was considered necessary to undertake a systematic revision of the bivalves of the Fox Hills Formation before attempting paleoecological studies. Redefinition of the species in accordance with the concepts of population systematics takes into account information on stratigraphic and lateral distributions, morphological variation, associated species, and inferred

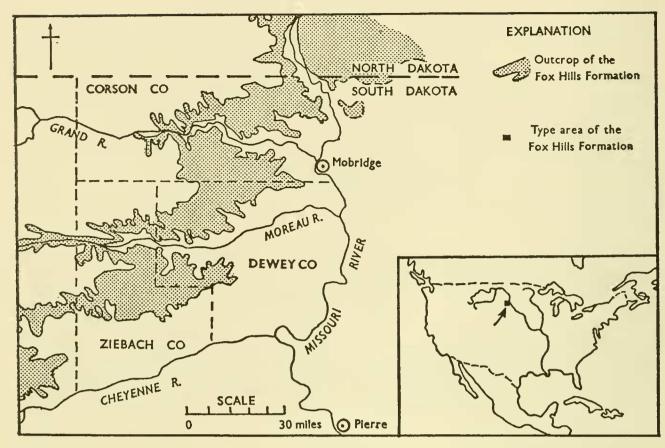


Fig. 1. Location of the type area of the Fox Hills Formation within the United States, and the outcrop of the formation in the Missouri Valley, South Dakota. (After Waage, 1961, modified.)

ecological preferences. Each species, when represented by a sufficient number of specimens, is documented by measurements and illustrations. Although this systematic study represents a major nomenclatural revision, the revision of other Upper Cretaceous faunas is required before the preparation of meaningful species synonymies or refinement of correlations are possible.

The stratigraphic distribution of the species and their gross relative abundance in the biostratigraphic units of the Fox Hills Formation are shown in Figure 4. Full details of the stratigraphic and geographic distributions, the numerical and relative abundance of species in fossil assemblages, and of the faunas of the biostratigraphic units will be given and discussed in a series of paleozoological papers. A list of the localities and maps showing their distribution are given in the companion *Bulletin* 27 of Waage (1968) which should be consulted for all stratigraphic information.

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studies outside New Zealand and to my wife, Erica, for her practical assistance and encouragement.

This study of the Fox Hills bivalves was undertaken on the suggestion of Prof. K. M. Waage, Yale University, who has given constant advice and close collaboration. His stratigraphic mapping of the type area of the Fox Hills Formation provided the essential basic framework for the study. Prof. A. L. McAlester of Yale University shared freely his knowledge of bivalves and guided the course of the work. The source and development of ideas is always difficult to accredit, and I owe a great deal to these two co-workers.

I gained much from discussions on paleoecology and ecological philosophy with Dr. J. F. Mello, U. S. Geological Survey, and Dr. M. A. Buzas, U. S. National Museum. Dr. Copeland MacClintock, Yale University, greatly facilitated the descriptions of the shell structures. I am most grateful to the following for assistance with collections and types: Drs. Erle Kauffman, and D. F. Squires, U. S. National Museum, Dr. N. F. Sohl, U. S. Geological Survey; Dr. H. G. Richards, Academy of Natural Sciences, Philadelphia; Dr. W. P. Popenoe and Takeo Susuki, University of California; Drs. A. J. Boucot and H. A. Lowenstam, California Institute of Technology; Dr. J. A. Jeletzky, Geological Survey of Canada; and Dr. P. S. Warren, University of Alberta. David Harvey, now at the University of Alberta, and David Keith, then at the Peabody Museum, Yale University, assisted with technical matters, and John Howard, then photographer at Peabody Museum, and N. S. Beatus, photographer, New Zealand Geological Survey, gave freely of their time and advice. The curation of the extensive collections is largely due to the efforts of Mrs. C. Stearns, Bentley Howard, Robert Richardson and Michael Nedila, all from the New Haven area. The manuscript benefited greatly from valuable suggestions and constructive criticisms of Prof. Léo Laporte, Brown University, and Dr. Erle G. Kauffman, U. S. National Museum.

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STRATIGRAPHIC SETTING

The Fox Hills Formation consists of shallow-water marine sediments which represent a late phase in the withdrawal of a sea that fluctuated in size through Cretaceous time (Cobban and Reeside, 1952; Reeside, 1957). Major movement of the west shoreline was eastward regression, interrupted by westward transgressions due to sudden "subsidences of the single sedimentary basin" (Weimer, 1960), with the supply of sediment not exceeding subsidence till near the end of the Cretaceous.

Correlation of the Fox Hills Formation with the biostratigraphic divisions of the standard European Maestrichtian sequence is uncertain (Waage, 1968). Cobban and Reeside (1952, p. 1026) and Reeside (1957) consider it of "upper Maestrichtian" or "middle and later Maestrichtian" age respectively. Jeletzky (1962) correlates the formation with the late lower Maestrichtian ("lower part of Belemnella cimbrica zone?"), although in his Figure 1 he shows the formation extending into the Upper Maestrichtian. Precise correlation must await a fuller knowledge of the stratigraphy and faunas of both European and Western Interior sequences.

LITHOSTRATIGRAPIC UNITS

In the type area the Fox Hills Formation consists of 300 to 350 feet of dominantly silty and sandy sediments transitional downward into the Pierre Shale and upward into the mainly terrestrial beds of the Hell Creek Formation. In recent years a fourfold lithostratigraphic subdivision of the type Fox Hills into the Trail City, Timber Lake, Bullhead and Colgate members has been accepted by the South Dakota Geological Survey and other workers (Waage, 1961, 1964). Waage (1968) has shown that the complexity of lateral facies changes, the lateral discontinuity of units, and the occurrence of transitional lithologies prevent recognition of the four characteristic lithologies over the entire type area and outside its limits. Consequently, he has proposed a hierarchy of members and lithofacies units to describe the depositional history of the area.

Waage (1968) delimits three members: a lower clayey silt unit (Trail City Member), a westward-tapering sand body (Timber Lake Member), and an overlying unit (Iron Lightning Member) of intricately related banded beds (Bullhead

lithofacies) and bodies of fine- to medium-grained clay sandstones that weather to a fluted light-gray color (Colgate lithofacies) which thickens westward (Fig. 3). The three members can be mapped individually only in the eastern part of the type area. To the west the Timber Lake Member is absent, and to the northeast in North Dakota the Trail City Member is very thin or absent. The Iron Lightning Member is thickest in the west and oversteps the older formations eastward. The sediments and faunas of the members indicate a close relationship between the Trail City and Timber Lake members and permit classification of the members into two environmental categories: shallow-shelf deposition for the Trail City and Timber Lake, and inshore marine- and brackish-water deposition for the Iron Lightning Member.

Second-order sedimentary characteristics permit subdivision of the members into lithofacies units. The Trail City Member is subdivisible into a Little Eagle and an Irish Creek lithofacies; the latter outcrops mainly west of but also extends around the southern and eastern flanks of the former (Waage, 1968, figs. 16–18). Irish Creek lithofacies also intertongues with the lower part of the Timber Lake Member along its western margin. The Trail City Member becomes sandier eastward, giving an indication of the downward and southward encroachment of the Timber Lake sands in this region. Waage discusses only one very local lithofacies (Rock Creek) of the Timber Lake Member. This occurs along the western Grand River, where it is transitional with the underlying Trail City, and consists of alternating thin-bedded mudstone and sandstone and sandy mudstone. Another lithofacies is represented by the current-bedded, less muddy sands of the *Tancredia-Ophiomorpha* Biofacies. There are other lithofacies, but these are less distinct and not as pertinent to fossil distributions.

The Iron Lightning Member consists of two distinct but genetically related lithofacies: (1) alternating sandstones and mudstones of Bullhead lithofacies (the banded beds of authors), and (2) whitish-weathering sandstones of Colgate lithofacies. Waage (1968, p. 116) has described the distribution of these units as follows:

Along the Grand River and northeastward from the type area of the Fox Hills into the Missouri Valley area of North Dakota the sand lithofacies occupies the upper part and the thin bedded or "banded" lithofacies the lower part of the Upper Fox Hills sequence. . . . the simple vertical succession does not hold south of the Grand River. In the Moreau valley area and beyond, the sand lithofacies recurs at more than one level in the westward-thickening Upper Fox Hills sequence and as many as 3 "Colgate" sands separated by banded beds may be present locally. The uppermost sand is commonly but not everywhere the thicker. One or all sands may be absent locally through lateral change to the banded bed lithofacies or, for the uppermost sand only, through removal by local channeling prior to the deposition of the overlying Hell Creek. . .

Formation. The upper contact of the Fox Hills Formation with the overlying Hell Creek Formation is arbitrarily taken at the first appreciable bed of lignite or lignitic shale.

The relationships of the units recognized in the type area of the Fox Hills Formation are given in Figures 2 and 3, and their characteristics are summarized as follows:

Trail City Member—65 to 210 feet of light-gray-weathering clayey silt, which is subdivisible into two lithofacies:

- 1) Little Eagle lithofacies: clayey silts becoming more sandy near the top and eastward, characterized by a mottled texture produced by organic reworking of the sediment, a consequent lack of bedding, and in its lower half layers of calcareous
- concretions, many of which are highly fossiliferous.

2) Irish Creek lithofacies: similar light-gray clayey silt and some fine-grained sand characterized by an absence of abundant fossiliferous concretions and with thinly interbedded clay and silt throughout much of the lower part which is the lateral equivalent of the Little Eagle lithofacies. The upper part of the Irish Creek, locally laterally equivalent to part of the Timber Lake Member, contains fine-grained sand as well as silt, is thin bedded locally; reworking by organisms is common. Fossils are common only in this upper reworked portion of the Irish Creek lithofacies. They occur mostly in an extension of the concretion layers of the Cucullaea Assemblage Zone of the Timber Lake Member in the Moreau Valley and in its lateral variant in the Grand Valley.

Timber Lake Member—generally about 50 to 100 feet thick, but with marked local variation in thickness. The member thins to the southwest and west, thickens north-westward, is lithologically more complex than Trail City Member, and is characterized by yellow-brown to yellow-orange-weathering muddy sands (subgraywacke) and large dark-reddish-weathering concretions. It has two main subdivisions: a lower and thicker part with layers of concretions, many of which are richly fossiliferous and contain diverse faunas, and an upper part (Tancredia-Ophiomorpha Biofacies) of generally slightly coarser and more pure sands, commonly cross-bedded, in which a distinctive fauna of low specific diversity occurs as shellbeds and scattered specimens in matrix. There is also a third local unit of thin-bedded sediments (Rock Creek lithofacies) which is a variant of the more muddy sands transitional between the Trail City and Timber Lake members.

Iron Lightning Member—about 58 to 170 feet thick but variable because of local facies changes, consisting of two intimately related lithofacies:

- 1) Bullhead lithofacies: between 35 and 110 feet of light-brown-gray-weathering sand, silt and clay, with a wide range of sedimentary structures. The sandy beds sometimes contain platy calcareous concretions. Plant fragments, scattered throughout layers, concentrated on bedding planes, and locally as lignitic laminae, are abundant. Fossil assemblages are uncommon, generally fragmented, and of low specific diversity.
- 2) Colgate lithofacies: lentils and tongues of fine- to medium-grained friable sandstone with considerable interstitial clay that weathers to characteristic fluted gray-white outcrops, and locally contains large spheroidal brown-red-weathering concretions. Larger bodies of sand, up to 60 feet thick, form the upper part of the member in most sections, but sand bodies up to 20 feet thick occur as lentils in the lower Bullhead lithofacies. The lithofacies is characterized by shellbeds of Crassostrea and channel-fills with abundant Corbicula and other faunal and floral remains. Plant remains are abundant.

The geology of the areas adjacent to the type area of the Fox Hills is poorly known. Glacial deposits largely mask the sequence east of the Missouri River. Southwest, about 50 miles along the outcrop north of the Cheyenne River, the for-

mation changes lithofacies into a heterogeneous sequence of dominantly sandy nonmarine beds. As stated by Waage (1964, p. 544):

This complex and little known [sequence] occupies a large area of outcrop in and south of Meade County, between the type area and the Black Hills (Fig. 1). Here the formation rests about 250 feet lower in the section relative to the top of the range zone of *Baculites clinolobatus* than does the base of the Fox Hills in the type area. Although the details are unknown, the gross relationships indicate that this brackish and continental phase of the Fox Hills was a large delta or series of coalescing deltas formed by major drainage into the Cretaceous sea from the north or northwest. [It] was established while Pierre Shale was deposited in the area of the type Fox Hills, and it marks the westward limit of the sea in this part of the interior region during the deposition of the type Fox Hills.

BIOSTRATIGRAPHIC AND BIOFACIES UNITS

The units recognized and defined by Waage (1968) are used in this paper and are shown in Figures 2 and 3. They include assemblage zones, named and unnamed concretion layers and biofacies.

The assemblage zones consist of a layer or a group of layers of fossiliferous and unfossiliferous concretions with each assemblage zone being separated by an interval of sediments devoid of concretions or containing only a few mostly unfossiliferous concretions. In each assemblage zone the area of distribution of richly fossiliferous concretions is restricted. Some assemblage zones have a marginal fringe of scattered sparsely fossiliferous concretions and very rare richly fossiliferous concretions, but all become barren laterally (Fig. 3; also illustrations of Waage, 1968). No continuous concretion layers can be recognized in the *Tancredia-Ophiomorpha* sands or in Iron Lightning Member.

As emphasized by Waage, the most distinctive characteristics of the assemblage zone are the dominance of each by one or few species and the occurrence in each of a different and distinctive assemblage of dominant species. Most species occur in all assemblage zones, and concretions dominated by the same species may occur in several. But in only two assemblage zones, the Lower and Upper nicolleti, are the same few species dominant. This is an example of a recurrent assemblage zone. Assemblage zones in the sense used here fall within the definition of Assemblage Zones of the American Code (Am. Comm. Stratig. Nomenclature, 1961, Art. 21) and are named for one or two of the dominant and widespread species characteristic of the zone. Although they are biostratigraphic units they also qualify as key beds under the classification of rock-stratigraphic units (Am. Comm. Stratig. Nomenclature, 1961, Arts. 8, 19e). The faunal unity of the assemblage zones and the fact that they transgress lithofacies (Fig. 3) also mean that they are biofacies if this term is used in the sense of "sediments characterized by a distinctive fauna" (Weller, 1960).

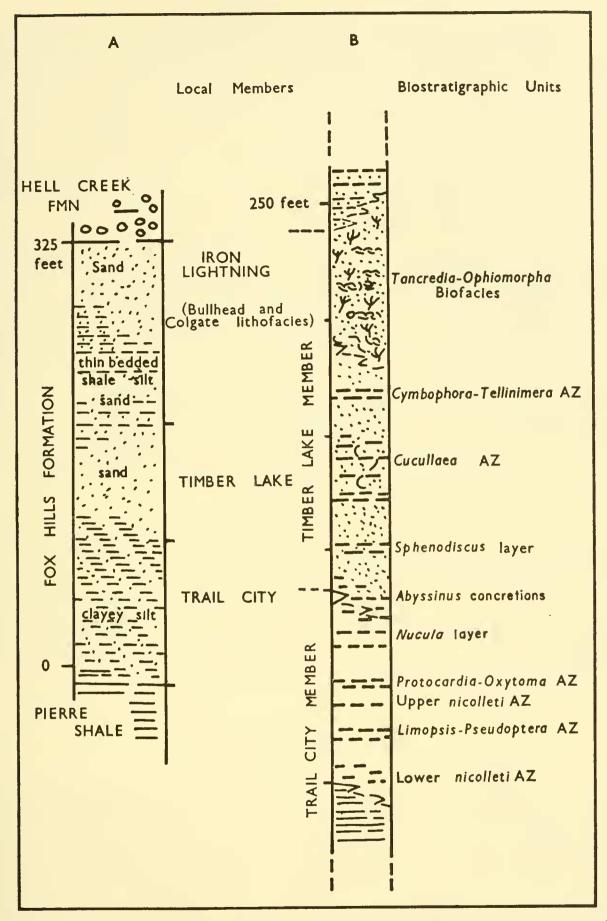


Fig. 2. Diagrammatic columnar sections of the lithostratigraphic units of the Fox Hills Formation (A) and the biostratigraphic and biofacies units within the Trail City and Timber Lake members (B) in the type area, north-central South Dakota. AZ = assemblage zone. (After Waage, 1961, modified with additions.)

Concretion layers characterized by a fossil name, such as the *Nucula* layer and the *Sphenodiscus* layer, are distinguished from assemblage zones largely by the relative abundance of fossils. In these layers the concretions are generally barren and the rare fossiliferous concretions contain only a few specimens. Biofacies are defined as stated in the previous paragraph, and consist of a more heterogeneous mixture of sediments containing random occurrences of fossils which form a distinctive suite. That these assemblage zones, biofacies and concretion layers represent different environmental conditions, and hence are extremely useful in paleoenvironmental reconstructions, is documented by Waage (1967, 1968), and will be further discussed by this writer in a separate publication.

By utilizing key beds of bentonite, glauconite and jarosite to give a stratigraphic framework related to the concretion layers, Waage has shown that most assemblage zones in the Trail City Member and in the lower part of the Timber Lake Member are essentially isochronous. There are two important exceptions:

- 1) The upper Trail City Member of the Grand River Valley and the lower Timber Lake Member of the Moreau Valley contain a number of disjunct concretion layers of small extent that occur at progressively higher horizons southward across the type area, more or less along the transitional contact of the members. Other than its time-transgressive relationship, this zone of concretion layers is comparable in its general features to the isochronous assemblage zones above and below. The concretions are characterized by a distinctive fauna dominated by small ammonoids, especially *Discoscaphites abyssinus*, and have been called abyssinus concretions or layers by Waage (1968).
- 2) The very shallow-water, often intertidal, more pure, generally cross-bedded sands forming the upper part of Timber Lake Member are complexly related to the remainder of the member. These complex sands contain a distinctive fauna of low diversity dominated by shellbeds of the thick-shelled bivalve *Tancredia americana* and the trace-fossil *Ophiomorpha*, a burrow probably made by a *Callianassa*-like crustacean. The occurrence of the characteristic fossils throughout the intertonguing lithofacies prevents the recognition of isochronous subunits but distinguishes a faunal unit named *Tancredia-Ophiomorpha* Biofacies.

PALEOENVIRONMENTAL SETTING

The known regional pattern of lithofacies in western South Dakota indicates that in the type area of the Fox Hills Formation the sediments were deposited close to the margin of the Maestrichtian sea and only about 50 miles northeast of a large deltaic complex. In the type area the gross environment of deposition of the members is indicated by the characteristics and relationships of the lithofacies and their contained faunas; namely, shallow-water shelf for the Trail City and Timber Lake members, culminating in littoral deposition of the strongly cross-bedded uppermost part of Timber Lake Member (*Tancredia-Ophiomorpha* Biofacies), shallow bay, intertidal, and perhaps closed bay for Bullhead lithofacies, brackishwater, estuarine, tidal or river channel deposition for Colgate lithofacies, and the mostly terrestrial lignitic sequences in the overlying Hell Creek Formation.

As documented by Waage (1968) the sequence of lithofacies and their faunas is due to the interaction of two different gross environments of deposition: initiation, growth, and southward spread of an offshore marine sand body (Timber Lake Member) within the area of deposition of shallow-shelf silty muds (Trail City Member), with the sand body being overlapped by an eastward-spreading complex of inshore marine and nonmarine deltaic sediments (Iron Lightning Member and Hell Creek Formation). Shallow-water marine shelf deposition prevailed through Trail City and Timber Lake time. Gradual shallowing due to the growth of the sand body culminated in the partly littoral marine deposits of the locally strongly cross-bedded uppermost part of the Timber Lake Member (Tancredia- Ophiomorpha Biofacies). This sand body appeared near the top of the Trail City Member at the level of the upper jarositic zone, and by Sphenodiscus concretion layer time covered all of the eastern part of the area (Waage, 1968). To the west the Irish Creek lithofacies apparently accumulated behind the growing barrier, possibly in a shallow bight. Cessation of the southward advance of the sand body in Cymbophora-Tellinimera Assemblage Zone time coincides closely with the appearance in the west of the Bullhead lithofacies just above the Cucullaea Assemblage Zone. This shallow-water marine inshore lithofacies and its associated often brackish-water sand bodies of Colgate lithofacies spread rapidly eastward, overlapping a large part of the Timber Lake sand body. Continued regression led to the deposition of the largely nonmarine sediments of Hell Creek Formation over the western part, and perhaps over all of the type area.



OCCURRENCE OF THE FOSSILS

A characteristic of the Fox Hills Formation in its type area is the occurrence of fossils in two major ways. In the Trail City Member, and lower part of Timber Lake Member, most fossils occur in calcareous concretions, many of which are richly fossiliferous. Fossils are uncommon in the sediment and are usually associated with the concretion layers. In the Iron Lightning Member, and in the uppermost part of Timber Lake Member (Tancredia-Ophiomorpha Biofacies), the fossils occur in shellbeds or as specimens scattered through the matrix, and fossils in concretions are rare. The Colgate lithofacies is notable for the presence of shellbeds of Crassostrea and Corbicula.

Waage (1968) has fully described the morphological characteristics of the concretions. Most are oblate, spheroidal, or subtabular. A few are irregular in shape. The two longest axes of most concretions parallel the bedding surface. The axes show no preferred orientation either locally or regionally within a layer. Concretions range in size from less than one inch to more than six feet maximum dimension. Only rarely, and particularly in Colgate Member, does the maximum measurement exceed two feet. The height of most concretions is less than 12 inches. Most concretions have an outer soft (punky), partly calcified jacket which is sometimes separated from the hard core by a zone of calcitic minerals and gypsum.

A layer of concretions at any one locality contains barren, sparsely fossiliferous (one to 10 to 20 specimens), and richly fossiliferous (containing several hundred to a few thousand specimens) concretions, with the proportions of the three categories varying considerably within short distances. Barren concretions generally are the most numerous, although at a few localities every concretion is richly fossiliferous. Sparsely fossiliferous concretions are always few in number. In each concretion layer, or group of layers, the area of distribution of richly fossiliferous concretions is restricted. Some have a marginal fringe of scattered sparsely fossiliferous concretions and very rare richly fossiliferous concretions, but all become barren laterally (Fig. 3).

Counts show that the assemblages of most fossiliferous concretions are dominated by one to three, and very rarely four, species of molluscs, mainly bivalves. Adjacent concretions in a layer are dominated by the same few species. In a layer at one locality, a single concretion may be dominated by Species A, an adjacent concretion by species A, B, or rarely C, the next by B, and others by combinations of AB, BC, AC, ABC. Assemblages dominated by a few species, whether

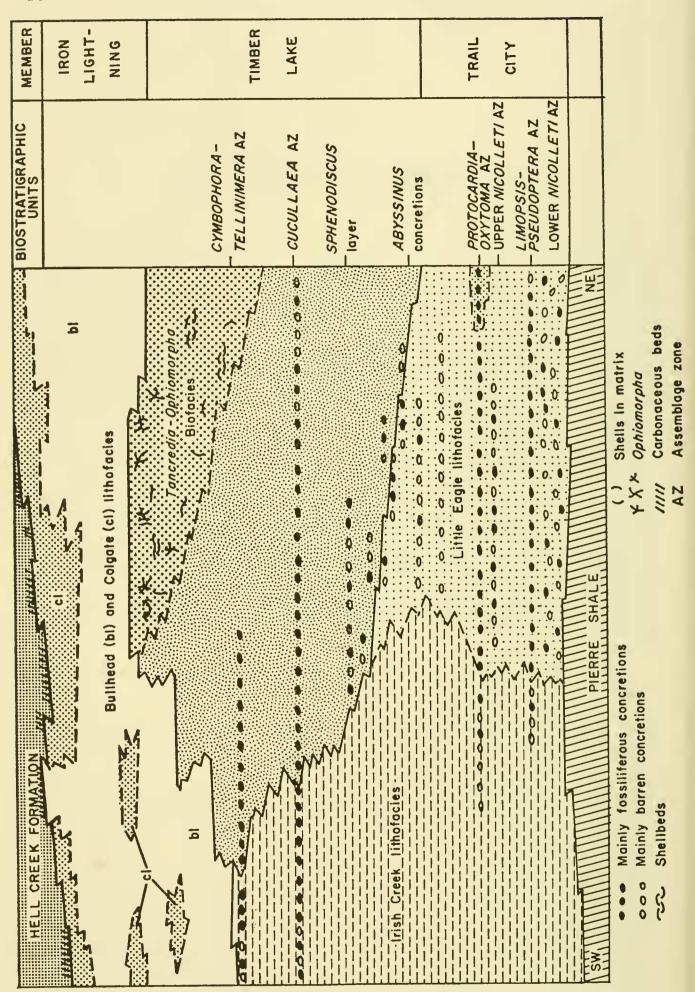


Fig. 3. Schematic cross-section of the Fox Hills Formation showing the relationships of the lithostratigraphic and biostratigraphic units along a southwest to northeast section. (See Waage, 1968, especially figure 12, for additional information.)

in concretions or shellbeds, are here called associations and are named after the dominant species. The dominant species are present everywhere over the geographic extent of the layer, or group of layers, resulting in marked taxonomic dominance by a few species even though the diversity of species may be high. In each concretion layer, or group of layers, less than six species comprise between 53 and 91 percent of the counted fauna and less than six associations form between 60 and 100 percent of the number of occurrences of associations recognized.

In lithostratigraphic units where the fossils occur in matrix the assemblages are also dominated by one or two species.

In the richly fossiliferous concretions the fossils usually are densely packed and randomly oriented (Pls. 40–42), although in concretions dominated by one of the inequivalve compressed epifaunal species such as Oxytoma, Pseudoptera, Phelopteria and Tenuipteria the specimens sometimes tend to be aligned, often subparallel to the bedding direction. This is most obvious in the Timber Lake Member. Where an assemblage is formed by many species, say 10 to 30, the range of sizes of specimens varies markedly. However, assemblages dominated by one or two species frequently consist solely of specimens of a very restricted range of size classes which clearly represent one or two spatfalls.

PRESERVATION

Very well-preserved specimens are normal in most assemblages in all stratigraphic units. Many specimens are colored or color-banded, and a large number retain ligament material, periostracum, or both. Specimens are easily extracted from concretions except in the case of some concretions containing few specimens which have been partially recrystallized.

Fossils in the matrix of Trail City Member and Bullhead lithofacies, even when adjacent to or projecting from concretions, are mostly crushed. Specimens from the less compactible sands of Timber Lake Member, especially Tancredia-Ophiomorpha Biofacies, Bullhead lithofacies and Colgate lithofacies, are usually only slightly crushed or distorted. The fossils in the outer one-eighth to one-half inch zone of the core of some concretions in Lower nicolleti Assemblage Zone, and rare ones in other units, may be slightly crushed. The fossils in the core of concretions are not distorted, although very rare and usually small concretions less than eight inches in diameter may have slightly distorted fossils throughout.

Worn shells and shell fragments are present but rare in most assemblages in the Trail City and Timber Lake members. Broken specimens are present in every assemblage; however, the pieces usually are present in the assemblage, often only a few millimeters apart. In *Tancredia-Ophiomorpha* Biofacies and the Iron Lightning Member worn shells and broken fragments are common at some localities and reflect the higher energy environment.

Disarticulated valves are numerous only in the *Tancredia*, *Crassostrea* and *Corbicula*, and less commonly in the *Dosiniopsis* shellbeds of *Tancredia-Ophiomorpha* Biofacies and Iron Lightning Member. In the concretions of Trail City and Timber Lake members the articulated specimens, either slightly gaping or

tightly closed, are more numerous than single valves. This applies both to infaunal equivalve and epifaunal inequivalve compressed species. Rare species, especially those represented by less than 10 specimens per assemblage, tend to occur more commonly as single valves, although double valves frequently dominate and are more common than is usual in fossil occurrences. Species forming an assemblage may have slightly different disarticulation to articulation and left to right valve ratios. These small differences can be explained by biological factors, primarily the size of the shell and strength of the ligament, or time of death, rather than by different histories of transportation.

The large number of closed specimens correlates with the common occurrence of specimens which are hollow or partially or completely filled with calcitic minerals (Pl. 5, fig. 10); i.e. the closed valves of *Oxytoma* almost always contain a calcitic filling (Pl. 15, figs. 3–4). Where sediment partially fills shells it is restricted to the stratigraphically lower part.

DEGREE OF TRANSPORTATION OF THE ASSEMBLAGES

Some transportation of the assemblages preserved in the concretions of the Fox Hills Formation is indicated by their aggregation into masses (clearly not a life position) the admixture of species having different modes of life, the clustering of species into different parts of a concretion, traces of fine lamination in the jackets of some concretions, and the presence of broken specimens, seeds, plant fragments, fish remains and other organisms. That transportation, sublevation and differential sorting were slight, and burial rapid, is shown by the excellent preservation, high degree of articulation and the association of matching valves, the low proportion of broken specimens, the occurrence in assemblages of species of greatly different sizes, the general random orientation of infaunal (Pl. 5, figs. 9–11) and epifaunal species in assemblages, the clustering of different species into different parts of a concretion and the occurrences of different ranges of size frequencies of a species in one and in adjacent concretions (Pl. 15, figs. 1–4). The last two features, clustering and size frequencies, are very important for they highlight the negligible transportation and dispersal of life units.

Most assemblages in Trail City and Timber Lake members have undergone minimal transportation. There is evidence of greater transportation for some shellbeds in *Tancredia-Ophiomorpha* Biofacies and Iron Lightning Member. The shellbeds are often thin discontinuous layers containing slightly to well worn valves concentrated mainly concave down. Numerous articulated specimens are present in the *Tancredia* beds and in the *Corbicula* beds of Colgate lithofacies, and the *Crassostrea* beds of Colgate lithofacies have all the characteristics of present-day oyster banks.

The characteristics and faunal unity of the assemblages favor burial in the environment in which they lived. This is compatible with the observations of Ginsberg (1956), who showed that for the high energy Florida Reef skeletal grains greater than one-eighth of a millimeter in diameter accumulate in the same environment.

STRATIGRAPHIC DISTRIBUTION

Figure 4 summarizes the stratigraphic occurrence and the gross relative abundance of species in the units of the Fox Hills Formation.

Most species range throughout the lower part of the formation up to at least the base of the Tancredia-Ophiomorpha Biofacies. In this interval only five species are restricted stratigraphically: Clisocolus moreauensis, Protocardia sp. A, Sourimis equilateralis, Corbulamella gregaria and Cuspidaria moreauensis occur only in or below Protocardia-Oxytoma Assemblage Zone. Those species which range through the formation become very rare in and above Tancredia-Ophiomorpha Biofacies. Ostrea translucida and Phelopteria linguaeformis continue to be common in Tancredia-Ophiomorpha Biofacies, and Dosiniopsis occurs mainly in a zone at the base of the biofacies, although a few specimens were found also in the uppermost assemblage zones of Timber Lake Member. Crassostrea subtrigonalis and Corbicula sp. A are restricted to the Colgate lithofacies. No species are restricted to Bullhead lithofacies except perhaps the very rare Spisula? sp. indet. Its sparse assemblages are composed of species common in Trail City and Timber Lake members.

The striking feature of the stratigraphic distribution of the species is that most of the common and rare species are relatively abundant in only one stratigraphic unit. Only two species, *Protocardia subquadrata* and *Tenuipteria fibrosa*, are dominant in more than one unit although the following six species are common in two or more units (Fig. 4): the infaunal *Nuculana scitula*, *Malletia evansi* and *Tellinimera scitula* and the epifaunal *Oxytoma nebrascana*, *Phelopteria linguaeformis* and *Ostrea translucida*.

A second feature of the stratigraphic distribution of the lamellibranch species is the uniform diversity of bivalve species in the units below Tancredia-Ophiomorpha Biofacies and the sudden drop in the number of species in Tancredia-Ophiomorpha Biofacies and overlying units. The number of bivalve species in the major units (excluding the Nucula layer) underlying the Tancredia-Ophiomorpha Biofacies ranges from 15 to 35. Only the geographically restricted and relatively sparsely fossiliferous Upper nicolleti Assemblage Zone (N = 15) and Sphenodiscus layer (N = 20) have less than 26 species. The number of species drops sharply to 15 in Tancredia-Ophiomorpha Biofacies, where more than six were found only at Locality 83, to 12 in Bullhead lithofacies, to eight in marine assemblages in Colgate lithofacies, and to one (Unio sensu lato) in the freshwater beds of Hell Creek Formation.

The maximum number of mollusc species at a LOCALITY varies between 22 and 36 for units below Tancredia-Ophiomorpha Biofacies, drops markedly in Tancredia-Ophiomorpha Biofacies where more than 12 occurred only at Loc. 83 (N = 23 species), to 17 in Bullhead lithofacies where more than four occurred only at Localities 56 and 224, and to eight in Colgate lithofacies. The maximum number of molluscan species in a concretion at a locality in Trail City and Timber Lake (exclusive of Tancredia-Ophiomorpha Biofacies) ranges between 22 and 27 per unit.

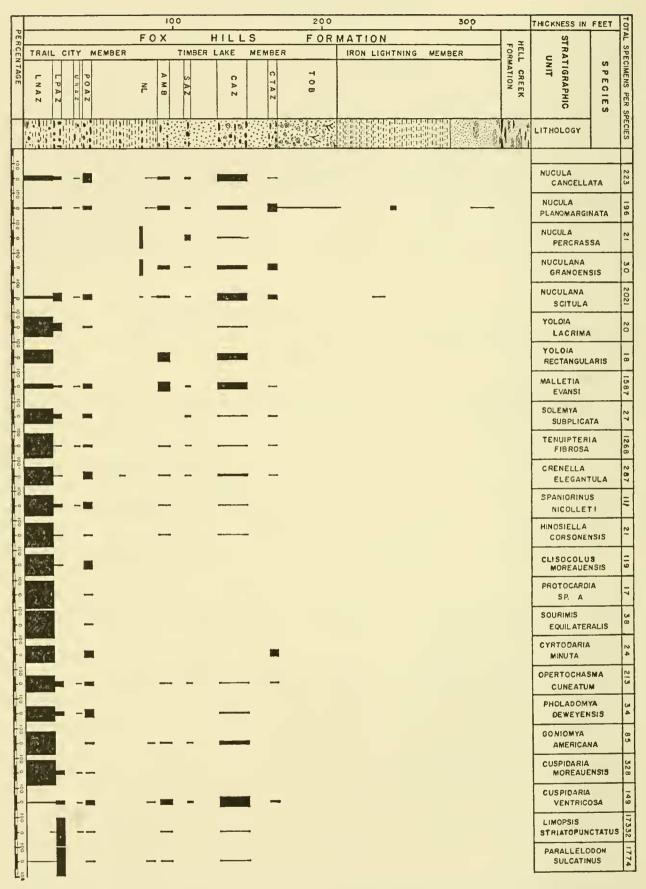


Fig. 4. Stratigraphic ranges and relative abundances of bivalve species in the Fox Hills Formation. Sb = shellbeds.

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PREVIOUS WORK ON THE BIVALVIA FROM THE TYPE AREA OF THE FOX HILLS FORMATION

Waage (1968) has discussed fully the early geological investigations of the type area of the Fox Hills Formation. Attention is drawn here to reports presenting

descriptions or lists of species.

Morton (1842) described two species common in the type area. Both were collected by Nicollet from localities some distance down the Missouri River. Evans, in 1849, collected the first fossils from the present type area. These were examined by Owen (1852), who identified four species of bivalves. Additional species, including eight from the type area, in the collections of Evans were later described by Evans and Shumard (1854, 1857). Even though the brief descriptions lack illustrations most species can be identified with confidence. The location of Evans and Shumard's collections is unknown and prevents the identification of three species, Avicula triangularis, Pholadomya elegantula, and Leda fibrosa. Meek and Hayden in 1853, at Hall's direction, collected Cretaceous fossils in the White River Badlands. They were described by Hall and Meek (1856), who listed six species, one of which, Pecten rigida, is common in the type area.

The major era of collection and description of species from the Upper Cretaceous of the Western Interior and from the type area of the Fox Hills Formation began with Hayden's expeditions in the upper Missouri region during 1854–1856, with Warren's to the upper Missouri in 1856, and to the Black Hills in 1857, with Raynolds' to the Yellowstone in 1859–1860, and culminated with the reports and descriptions of Meek and Hayden (1856a, b, c; 1857, 1858, 1860b, 1861). Meek and Hayden's productive cooperation is evidenced by valuable stratigraphic data collected and interpreted, and by the description of 89 species of lamellibranchs, including 19 from the type area, and four from Long Lake near the Missouri River, some 40 miles northeast of the type area. Later both Gabb (1861) and Meek

(1864a) proposed nomenclatural changes.

The culmination of the early work came with the publication of Meek's (1876) invaluable monograph on the invertebrate faunas of the Upper Cretaceous of the Western Interior. He described two new species, Corbula crassimarginata and Ostrea subalata, from the type area of Fox Hills Formation, and incorrectly proposed the new name pellucida for Ostrea translucida. Meek (1876) recorded from the type area 29 of the 58 species described in this report. Nine of the remaining 29 species were described from other historically important Upper Cretaceous localities in the Western Interior, mainly from Long Lake, Sage Creek, the forks of Cheyenne River, and Yellowstone River. Of the remaining 20 species, 11

are of uncertain specific status, seven are new, one (*Periploma subgracile*) was described by Whitfield (1877) from the Pierre Shale, Black Hills, and one (*Epilucina cedrensis*) was described by Stanton (1920) from the Cannonball Formation, North Dakota. All of these species are very rare and unlikely to have been found during the reconnaissance studies of Meek and Hayden.

Until this publication, Meek's monograph (1876) has been a standard reference for both American and foreign workers on Upper Cretaceous faunas. Important papers referring to species described in the monograph include Woods (1899–1913), Weller (1907), Gardner (1916), Stanton (1920), Wade (1926), Stephenson (1936, 1941, 1952, 1955), Popenoe (1937), Saul and Popenoe (1962). Meek's publication is of primary importance as it contains the first illustrations of most species described earlier, plus redescriptions, synonymies, and in many cases additional information. A classic for the time, it showed evidence of Meek's knowledge of recent species and problems of phenotypic variation, although he often returned to typological definitions of species. Its weaknesses are the general inadequacy of the descriptions for present-day comparative systematics, insufficient measurements, too few and often idealized illustrations, lack of stratigraphic data and the present uncertainty as to the whereabouts of some type specimens and original collections. Most of the descriptions and illustrations are more than adequate to identify species positively and to compile synonymies.

Since Meek's monograph little systematic work has been done on Upper Cretaceous Bivalvia of the Western Interior. His species concepts and names have been generally accepted, often erroneously, until now and have been used in numerous stratigraphic reports. The reader is referred to the systematic descriptions for references to nomenclatural changes made since 1876. Stanton (1920), in his description of the fauna of the Cannonball Formation (Paleocene), figured the holotypes of Nuculana scitula (Meek & Hayden) and Dosiniopsis nebrascensis (Meek & Hayden), described Lucina cedrensis, here recorded from the Fox Hills Formation, and showed the close similarity of the Fox Hills and Cannonball faunas. Cvancara's (1966) revision of the Cannonball fauna suggests an even closer similarity, notably for the protobranch species. Skogstrom (1959) discussed the paleoecological significance of Tancredia americana (Meek & Hayden). Invaluable information on the mode of occurrence and distribution of molluscs in the type area of the Fox Hills Formation is contained in the publications of Waage (1961, 1964, 1967, 1968).

REMARKS ON THE SYSTEMATICS

PURPOSE

This systematic study was undertaken to provide a basis for a paleoecological and paleoenvironmental study of the bivalve fauna of the Fox Hills Formation. Although the concepts of population systematics have been applied, the restriction of most species to one stratigraphic horizon or interval did not favor a detailed study of successive fossil populations. Where it was possible for a few of the dominant species, a comparison of simple statistical measurements (see below) made on fossil populations from several assemblages at a locality, from different localities and successive stratigraphic units showed no significant differences or trends. If the rates of evolution of the order of 0.5 to 2.5 million years for mollusc species being obtained by workers in the Cretaceous of the Western Interior (Gill and Cobban, 1966; Kauffman and Kent, 1968) apply, then the time of deposition for each of the pre-Tancredia-Ophiomorpha Biofacies and the Tancredia-Ophiomorpha Biofacies plus Iron Lightning Member parts of the Fox Hills Formation may not exceed some 2.5 million years. Indeed, the faunal and paleoenvironmental evidence suggest that the whole of the type Fox Hills Formation may span less than 2.5 million years.

PROCEDURES

Because of the abundance of material all stratigraphic units were heavily sampled, especially those below *Tancredia-Ophiomorpha* Biofacies in which the species show ecologically controlled geographic patterns. In the field detailed counts were made of the numbers of fossiliferous, sparsely fossiliferous and barren concretions, and also of shellbeds, in each stratigraphic unit at a locality. Assemblages were carefully sampled and whole or parts of concretions were broken down in the laboratory, the number of specimens of each species counted, and, if necessary, specimens selected for detailed morphological studies and measurement. More than enough specimens of the dominant species were obtained for a systematic study.

Many of the Fox Hills species are closely related to species described from Late Cretaceous sequences in other areas of the Western Interior. It is possible that many of these species represent distinct but overlapping segments of a lineage, perhaps subspecies or distinct species. Statistical variation studies on adequate successive samples of the "species" are required to determine their status. As this is well outside the scope of this study the species are discussed in general terms, and those thought to be conspecific or of subspecies rank are included in the synonymies but prefixed by an interrogation mark contained in square brackets.

MATERIAL AND DATA

All types and the bulk of the collections are housed in the Peabody Museum of Natural History, Yale University, New Haven, Connecticut, U. S. A. A small representative collection is held at the New Zealand Geological Survey, Lower Hutt, New Zealand, and a second at the Geology Department, School of General Studies, Australian National University, Canberra.

The collections are numbered according to a recently devised cataloguing system now applied to collections of invertebrate fossils. The entire collection from the type area of Fox Hills Formation and closely adjacent regions has the YPM accession number 7048. Localities with or without measured sections are numbered consecutively from 1 to 264 (Fig. 19). The reader is referred to Waage (1968) for all locality and section data. Because of the distinctive associations of species in adjacent concretions, collections from entire concretions, samples of concretions, or patches in matrix are allotted YPM Invertebrate Paleontology collection numbers, A206–799, 920–1406, a total of 1077 collections. Type and figured specimens and important specimens specifically mentioned in the text are allotted YPM specimen numbers.

Basic data, including measurements and tables presenting lists of all species, the occurrence and numerical and relative abundance, expressed as percentage, of species in concretions, samples, and stratigraphic units, and lists of localities at which each species occurs are deposited on open file at the Division of Invertebrate Paleontology, Peabody Museum of Natural History, Yale University.

For the 46 most common and better preserved species the following standard statistical data for each parameter were compiled and processed by an Elliot 503 computer via ALGOL programs prepared by Miss M. N. Newman, Applied Mathematics Division: total sample size (N), minimum value, maximum value, range, arithmetic mean (μ), standard deviation (s), variance (s²), and coefficient of variation (V) of sample. In addition, the coefficient of correlation (r) between parameters has been presented in a sample correlation matrix. Initially, the data were calculated for all fossil populations from samples in which the number of specimens exceeded the number of parameters measured. As there were no obvious differences between populations, the data for the available total sample of the species were processed. This total sample includes individuals of many age classes and different sexes from different paleoenvironments and geological times.

The total sample is heterogeneous, and the statistical data obtained from it cannot be expected to compare closely with data from homogeneous populations. For example, the values for V (coefficient of variation) are extremely high compared to those of recent species and many fossil mammal species (Simpson and others, 1960, p. 93).

The basic statistical data, excluding the sample correlation matrix, for the total sample of each species are given in the Appendix of this volume, and the full original data are held by the author. The measurement data given in each systematic description represent a further summary.

ABBREVIATIONS AND TERMINOLOGY

Abbreviations of the names of major institutions referred to in the text are:

ANSP — Academy of Natural Sciences, Philadelphia

CIT — California Institute of Technology, Pasadena

GSC — Geological Survey of Canada, Ottawa

UA — University of Alberta, Edmonton

UCLA — University of California, Los Angeles

USNM — United States National Museum, Washington

YPM — Peabody Museum of Natural History, Yale University, New Haven

Other abbreviations used are listed on the page preceding the plates at the back of this volume.

To avoid ambiguity the following terms are used in the text as defined here:

Assemblage—any aggregation of fossils, in concretions or matrix.

Association—an assemblage dominated by one or a few species, with all other species being subordinate.

Monospecific association—one in which more than 50 percent of the total numerical count consists of one species.

Dispecific association—one dominated by two species, each forming more than 25 percent of the total numerical count.

Polyspecific association—one dominated by three or four species, each forming about 25 percent of the total numerical count.

Qualitative allowance for biomass (Sanders, 1960) introduces a degree of arbitrariness into the minimal percentage value. Large species forming as low as 15 percent of the count are considered as codominant species.

Dominant species—a species forming more than 50 percent of the total numerical count of an association, with allowance being made for size and estimated biomass.

Codominant species—two or more species, each comprising more than 25 percent of the total numerical count of an association, with allowance being made for size and estimated biomass.

Subdominant species—a species forming between about 10 and 25 percent of the count of an association, with allowance being made for size and estimated biomass.

Because of their geographic ubiquity in a biostratigraphic unit these dominant and codominant species (taxonomic dominants) of associations are in this case also the "dominantly occurring" or characteristic species of Thorson (1957).

Lithofacies—one or more bodies of sediment or sedimentary rock distinguished from adjacent deposits by noteworthy lithologic and/or internal structural characters or both (Waage, 1968).

SYSTEMATIC DESCRIPTIONS

NUCULACEA

NUCULA

AUTHOR. Lamarck, 1799, p. 87.

Type Species. By monotypy, Arca nucleus Linnaeus (1758, p. 695), Recent, Europe.

Nucula cancellata Meek & Hayden (Plate 1, figs. 1-11)

Nucula cancellata Meek & Hayden, 1856a, p. 85. Meek, 1864a, p. 8. Meek, 1876, p. 102, Pl. 28, figs. 13a-e.

[?] Nucula assiniboiensis Landes, 1940, p. 131, Pl. 1, figs. 4-6.

DESCRIPTION. Shape typically nuculid, of medium-large size, specimens 4.1 to 24.6 mm long, equivalve, inequilateral, moderately to strongly inflated. Pseudolunule indistinctly separated from disc of valve, sometimes bounded by a faint narrow depression. Escutcheon lanceolate to heart-shaped, bounded by a ridge and depression of variable strength, strongest on gibbose specimens, mostly flat or slightly concave (especially at posterior end), rarely slightly convex and raised along commissure margin. Shape moderately variable; height, width and posterior length, respectively, 65.4 to 84 (N = 77, μ = 73.1%), 36.1 to 62.9 (N = 77, μ = 49%) and 23.7 to 44.2 (N = 77, μ = 33.1%) percent of length. Anterior margin rounded, the posterior end angular and the extremity situated at 48.2 to 68.5 (N = 77, μ = 57.8%) percent of height. Umbones blunt, flattened, opisthogyrous.

Shell ornamented with narrow radial U-shaped grooves and flat- to slightly convextopped costae four to five times as wide as the grooves, one-and-a-half to three costae per millimeter for specimens 15 to 20 mm long. Radial ornament crossed by irregular growth depressions and folds. First 1.5 to 2 mm of shell smooth; narrow radial grooves and sometimes fine concentric folds then appear. Periostracum marked by numerous microscopic crinkly striae which generally are eroded from the top of costae but stand out as fine ridges on the sides and floors of the grooves. Lunule and escutcheon with fine concentric striae only.

Hinge line two thirds to three quarters the length of dorsal margin, anterior part slightly convex, posterior part straight to slightly concave, with a known maximum of 22 anterior and 11 posterior teeth. Taxodont, teeth chevron-shaped, convex toward extremities, with a prominent keel for interlocking on convex side. Teeth larger, stronger and more widely spaced with distance from center. Small, weak, irregular and nodular teeth extend around dorsal margin of resilifer. Chrondrophore tooth on left valve large and

conical, distinct from next 3 to 4 closely spaced, bladelike, chevron teeth, matched on right valve by prominent pit. Resilifer short and wide, one fifth to one sixth of length of hinge, separated from the dorsal margin by a prominent plate, its axis opisthoclinally inclined at 20 to 30 degrees to anterodorsal margin, contains inner layer of ligament (Trueman, 1952, p. 203). Outer ligament extends about one third the length of the anterodorsal margin.

Muscle insertion areas deeply impressed in medium to large thick-shelled specimens. Adductor insertions subequal, subtriangular, situated close to dorsal margin, marked by prominent growth lines, and close to the inner margin are crossed by a narrow groove that parallels the longest axis. Posterior insertion area more elongate than the anterior, its long axis inclined prosoclinally at 40 to 50 degrees to hinge margin, bounded anteriorly by a prominent buttress. Anterior adductor buttressed along dorsal and posterodorsal margins. Pedal muscles (probably retractor-protractor-visceral muscles combined) unequal, close to commissure. Anterior insertion one-and-a-half to two times larger than posterior, open V-shaped with limb parallel to commissure margin four to six times longer than other limb, the axis of which parallels the margin of the anterior adductor. Posterior pedal insertion elongate triangular, tapering toward umbones, with wavy margins. Visceral muscle impressions form an L-pattern anterior to umbone, variable in number and shape even on matching valves of one individual, generally oval-circular. Muscle insertion areas between anterior adductor and oval ventromedian insertions commonly coalesced, the dorsomedian (elongated, narrow) and ventromedian most distinct, the former sometimes consisting of two impressions. One to four small impressions occur in the umbonal cavity above dorsomedian insertion, commonly coalesced with asymmetric patterns in right and left valves of one individual. Pallial line simple.

Valve margins strongly crenulated, one-and-a-half to three crenules per millimeter on moderately large specimens; crenules under the radial grooves, round-topped, as wide as U-shaped depressions between. Ostracum up to 2.5 mm thick, of two layers; a matte white finely crystalline outer layer forming one quarter to one sixth of total thickness (its inner surface costate) and an inner nacreous layer. Both layers often overthickened along ventral margin. Internal surface with striae and grooves. Many shells with a fawn to brown coloration and concentric color banding.

Types. Lectotype by subsequent designation of Meek (1876, in caption to Pl. 28, fig. 13a), USNM 434. Type locality: Moreau River, South Dakota. Stratigraphic position: Fox Hills Formation.

Neither the lectotype, reported by Meek to be a perfect specimen, nor the original of figure 13b are present in collection USNM 434. Their whereabouts is unknown. The other specimens are typical *cancellata*, and the lithology and associated species indicate that they were collected from the Timber Lake Member.

Types held at YPM are: hypotypes YPM 23946-48, 23950-52, 24130; and 23949 and 24502.

Discussion. The strength of the concentric ornament varies considerably. Strong thin growth folds and/or depressions, if present, give the shell a cancellate appearance. This may be intensified by the fine striae of the periostracum which by themselves also induce a faint cancellate ornament. On one specimen (YPM 24502) the position of the crenulations occurred under the grooves (normal) at the anterior end and along most of the margin but occurred under the costae along the posterior third. Crenulations are often evident on the external surface of a valve along the dorsal flank of prominent growth depressions. Some specimens have been partially (rare) or completely bored, probably by predatory gastropods, and the holes occur mainly in the upper third of the valve although exceptions are present. This general location is the most vulnerable as nuculids live shallowly buried with the dorsal margin approximately parallel to the mud/water interface (Yonge, 1939, fig. 2).

MATERIAL. 232 complete or largely complete specimens, mostly preserved as steinkerns.

Many specimens were broken during extraction from matrix. Only one specimen (Loc. 92, A799) is positively known to have been broken before or during transportation.

Occurrence. Normally as one or two specimens per concretion. Only two concretions contained more than six specimens: A1180, with 11, from Loc. 21, Protocardia-Oxytoma Assemblage Zone, and A788, with 10, from Loc. 90, an abyssinus concretion, Timber Lake Member. Approximately equal numbers were collected from the Trail City and Timber Lake members, although the ratio of disarticulated to articulated specimens was greater in the Timber Lake sands (1.46 to 0.61). This is compatible with the muddy sandstone lithology that would have been deposited under more turbulent hydrodynamic conditions. The lack of shell fragments and the percentage (41%) of articulated specimens argue against excessive transportation.

Nucula cancellata has been frequently reported from Upper Cretaceous sequences of the Western Interior, U.S.A. (White, 1879a; Griffitts, 1949; Robinson and others, 1959) and south-central Canada (Whiteaves, 1885; Gleddie, 1948).

COMPARISONS. N. cancellata is one of a group of closely related species characterized by prominent radial and concentric ornament and coarsely crenulated ventral margins. Clarification of its relationship to N. assiniboiensis, which appears to fall within the range of variation of cancellata, requires additional study.

Nucula planomarginata Meek & Hayden (Plate 1, figs. 12–18; Plate 2, figs. 1–3)

Nucula planomarginata Meek & Hayden, 1856a, p. 85.

Nucula planimarginata Meek & Hayden. Meek, 1864a, p. 8. Meek, 1876, p. 101, Pl. 15, figs. 8a, b; Pl. 28, fig. 16. Whitfield, 1880, p. 406, Pl. 11, figs. 5, 6. Stanton, 1920, p. 19, Pl. 1, figs. 2, 3. Cvancara, 1966, p. 293, Pl. 1, figs. 1–8.

[?] Nucula subplana Meek & Hayden, 1856a, p. 85. Meek, 1876, p. 99, Pl. 17, figs. 7a,b. Stanton, 1920, p. 20, Pl. 1, figs. 4-7.

[?] Nucula sp. Cvancara, 1966, p. 296, Pl. 1, figs. 9, 10.

DESCRIPTION. Shape typically nuculid, of medium-large size, specimens 3.8 to 24.3 mm long, equivalve, inequilateral, moderately inflated to compressed. Pseudolunule very narrow, indistinct; if distinct, separated from main disc of valve by a weak narrow ridge extending from umbone to anterodorsal angulation, ridge strongest along posterior third. Escutcheon heart-shaped, its margin ill defined except on very inflated specimens, when it is bordered by a sharp ridge internal to which is a depression that widens posteroventrally and a second umbonal ridge that fades before reaching commissure. Escutcheon surface convex, with a marked pout at commissure margin, the pout depressed at point of intersection with inner umbonal ridge. Shape moderately variable; height, width and posterior length, respectively, 66.9 to 83.5 (N = 80, μ = 15.9%), 26.7 to 54.1 (N = 80, μ = 41.9) and 22.7 to 42.1 (N = 83, μ = 30.1%) percent of length. Anterior end with a marked truncation, the posterior extremity obtusely rounded, situated at 48.8 to 69.9 (N = 73, μ = 60.5%) percent of height. Anterior and posterior to umbones are rows of dental socket pits, open to exterior only if the outer shell layers are absent, most prominent on thin-shelled specimens, and situated just outside pseudolunule ridge and just inside escutcheon ridge. Those in the escutcheon converge on depressed area of pout. Umbones prominent, narrow, strongly opisthogyrous and outcurving.

Shell ornamented by fine, closely spaced, irregular and crinkled, sharp-ridged concentric costae and growth striae of variable strength, and rare broad growth depressions. If strong the acute-ridged costae point dorsally. Escutcheon and anterior dorsoventral flanks with fine striae only. First 1 to 2 mm with very fine irregular concentric costae.

Hinge line about two thirds the length of dorsal margin, posterior and anterior segments convex, a known maximum of 28 anterior and 13 posterior teeth. Form of

teeth as for cancellata, larger, stronger and more widely spaced with distance from center, teeth of posterior segment extend up to a slightly more prominent chondrophore tooth at its anterior end. Ligament as for cancellata. Resilifer one sixth to one seventh the length of hinge, narrow and elongated, its axis opisthoclinally inclined at 20 to 30 degrees to anterodorsal margin, a dorsal plate is absent but a prominent posteroventral shelf occurs below the resilifer.

Muscle insertion areas weakly impressed, the posterior adductor impressed more strongly. Adductor insertions unequal, situated close to dorsal margin with about two thirds of their length projecting beyond ends of hinge, showing prominent growth lines and a narrow groove, parallel to longest axis, close to the inner margin. Posterior insertions oval, about two thirds to three quarters the size of anterior. Anterior insertion subtriangular. Pedal muscle insertion areas unequal, anterior about two to three times as long as posterior, both narrow, situated close to commissure margin. Anterior pedal scar sited under anterior third of hinge, open V-shaped with the limb parallel to commissure margin more impressed and three to four times longer than the other limb (visceral muscle attachment area), the axis of which is inclined to the dorsal margin of anterior adductor. Posterior pedal impression very elongated, narrow, tapers toward umbones, extends from end of hinge almost to resilifer. Visceral muscle impressions form an Lpattern, the dorsally directed limb situated further anteriorly than in N. cancellata, variable in numbers and pattern, mostly oval-circular, the dorsomedian and ventromedian most distinct, the former elongated and composed of two impressions fused to varying degrees. At least three impressions in umbonal region above dorsomedian scar. Pallial line simple.

Valve margins smooth, rare large specimens with faint crenulations. Ostracum up to 2 mm thick for large specimens, maximum thickness along ventral region, of two layers. A white finely crystalline outer layer, forming one fifth to one sixth of thickness, its inner surface with three to four faint radial costae per millimeter at 20 mm height, and a thick nacreous inner layer. Inner surface smooth, sometimes with faint radial striae. Many shells with a fawn to brown coloration and concentric color banding on some.

Types. Lectotype of N. planomarginata, USNM 347, by subsequent designation of Meek (1876, in caption to Pl. 15, fig. 8a), an incomplete specimen with poorly preserved shell, none of the outer surface remaining. Type locality: near Long Lake, Upper Missouri, North Dakota. Stratigraphic position: Fox Hills Formation. Lectotype of N. subplana, USNM 352, by subsequent designation of Meek (1876, in caption to Pl. 17, fig. 7a), a two-valved steinkern with an incomplete umbone on the right valve and the anteroventral margin crushed, L = 9.6, H = 6.9, W = 3.3, PL = 1.9 mm, figured by Meek (1876; idealized). Type locality: 150 miles up the Yellowstone River from mouth. Stratigraphic position: Upper Cretaceous.

Types held at YPM are: hypotypes YPM 23953-58.

Discussion. Large specimens are consistently more compressed than those of cancellata. The anterior two thirds of the inner margin of several of the largest specimens has faint short striations (Pl. 1, fig. 12), three to four per millimeter at a height of 20 mm. The "crenules" are developed over the radial costae of the inner surface of the outer shell layer and may represent an adaptation for interlocking the margins of the valve. The appearance of fine crenulations (pectinations of Vokes, 1949) on only the largest specimens emphasizes the dangers of using the presence or absence of marginal crenulations as a criterion for subgeneric or generic separation (see Cox, 1940).

The dental socket pits are marked by whitish dots on the surface of small specimens, but in larger specimens the pit is plugged by a rod of dark material, perhaps chitinophosphatic, that curves dorsally toward the exterior of shell at its tip, much in the manner shown by Trueman (1952, fig. 3) for the "horny process" present in N. nucleus (Linneaus).

MATERIAL. 207 complete or largely complete specimens, mainly as steinkerns. Many

specimens were broken during extraction. Ten were broken during or before transportation, and 10 from various locations were crushed by compaction.

Occurrence. Rarely more than three specimens in any one concretion from any member. The only exception was at Loc. 210 where most concretions sampled from the *Cucullaea* and *Cymbophora-Tellinimera* assemblage zones, Irish Creek lithofacies, contained more. The species is particularly numerous at Locs. 210 and 212 where 10 to 28 specimens were present in two concretions (A462 and 480) from the *Cymbophora-Tellinimera* Assemblage Zone.

The ratio of disarticulated to articulated specimens is greater in the Timber Lake sandstone, 1:46 compared to 0:6 for the Trail City silty mudstone, and this is compatible with the implied hydrological conditions. Little transportation is indicated by proportions of articulated specimens, lack of numerous broken specimens, and the excellent preservation of external shell surface.

Comparisons. Meek (1876) noted the presence of "very fine, irregular, radiating and minute concentric striae" on planomarginata and thought that the former would not be evident on well-preserved individuals. Although radial ornament is never visible on perfect specimens from the type area of the Fox Hills Formation, the slightest wear exposes the internal radial costae. The lectotype (USNM 351; Meek, 1876, Pl. 15, fig. 10) of obsoletistriata Meek & Hayden has a very pointed posterior end and a deep lunule. It represents a valid species. Stanton (1920) had difficulty in separating subplana from planomarginata. Several samples from the Timber Lake Member contain a range of specimens, the smaller of which match subplana and the larger planomarginata. Measurements confirm the opinion that subplana is based on a juvenile specimen of planomarginata.

Nucula percrassa Conrad (Plate 2, figs. 4–11)

Nucula percrassa Conrad, 1858, p. 327, Pl. 35, fig. 4. Weller, 1907, p. 369, Pl. 29, figs. 1-5. Gardner, 1916, p. 513. Wade, 1926, p. 39, Pl. 8, figs. 1-4. Richards, 1958, p. 59, Pl. 10, figs. 1, 2, 4.

Description. Large for the genus, specimens 8.2 to 34.8 mm long. Pseudolunule characteristics unknown. Escutcheon heart-shaped, indistinct, its margins marked by a sharp decrease in prominence of concentric ornamention. Shape variable; height, width and posterior length, respectively, 61.2 to 73 (N = 6, μ = 65.4 %), 42.9 to 46 (N = 2, μ = 44.5%) and 29.3 to 42.7 (N = 6, μ = 34.5%) percent of length. Both extremities rounded, posterior more pointed than for the above species, situated at 49.2 to 63.1 (N = 6, μ = 55.3%) percent of height. Ventral margin convex or with a slight sinuosity anterior to umbones. Umbones flattened, not prominent, opisthogyrous.

Shell ornamented with very fine radial costae, 1.5 to 3.2 per millimeter on large specimens, which coincide with dark lines within the shell and are separated by flattopped interspaces six to eight times as wide as costae. Radial ornament crossed by microscopic discontinuous crinkly striae, growth costae of variable strength and regularity, and sometimes by prominent growth depressions. Prodissoconch smooth. Periostracum with microscopic, discontinuous crinkly striae. Hinge poorly exposed, general morphology as for above species, about one half to two thirds the length of the dorsal margin, both segments straight or slightly convex, posterior sometimes slightly concave anteriorly, with a known maximum of 27 anterior and 11 posterior teeth. Muscle insertion areas strongly impressed on thick-shelled specimens, especially the adductors, dorsomedian and ventromedian insertions. Form and distribution as for cancellata. Posterior adductor with a strong broad buttress along anterior margin. Pallial line simple.

Valve margins crenulated, 1.5 to 3.0 per millimeter on large specimens, crenules under interspaces, semiconical-shaped, highest and widest at margin of valve, one to

one-and-a-half times as wide as depressions. Shell with a vitreous and polished appearance. Layering and thickness as for *cancellata*. The inner surface of outer layer has prominent round-topped costae, the outer surface shows faint crenulations at growth pauses and even fainter scalloping due to changes in color of shell. Inner surface of inner layer faintly striate. Some shells with fawn coloration and color banding.

Types. Lectotype by subsequent designation of Johnson (1905, p. 7), ANSP 16710, a steinkern figured by Conrad (1858, Pl. 35, fig. 4). Type locality: Owl Creek, Mississippi. Stratigraphic position: Owl Creek Formation.

Types held at YPM are: hypotypes YPM 23959-62.

Discussion. Compaction distortion and crushing prevent trustworthy assessment of the variation of shape of this species. Undistorted specimens from Loc. 53 have smaller H/L percentages than any others.

MATERIAL. 21 specimens, steinkerns and with shell, mostly incomplete and distorted by compaction, the incompleteness being due to extraction. For stratigraphic distribution see Figure 4.

Occurrence. No more than two specimens were collected from any one concretion. The ratio of disarticulated to articulated specimens at Loc. 25 is 1.29:1, and indicates slight transportation. The species is virtually restricted to the *Nucula* layer at Locality 25 where it is associated with a distinctive assemblage of mostly infaunal species. A codominant in this assemblage, *Nuculana grandensis*, is also significantly more numerous at Loc. 25 than elsewhere. An association with a preferred habitat is suggested.

This is the first record of N. percrassa from the Western Interior.

Comparisons. The characteristic ornamentation, polished-vitreous appearance of the shell, position and shape of the crenulations, and low H/L ratio distinguish this species from N. cancellata. Visual and measurement comparison with the type and a suite (YPM 3441, 3463, coll. C. O. Dunbar) of percrassa from the Ripley Formation, Coon Creek Tongue, McNairy County, Tennessee shows that the Fox Hills specimens are conspecific. The Coon Creek specimens, although possessing a greater diversity of shape, particularly the degree of incurving of the ventral margins, have the same characteristics quoted above and a similar pattern of pedal muscle insertion areas.

Nucula slackiana Gabb (1860) from New Jersey, Maryland and Virginia has the same characteristic ornamentation, crenulations and polished-vitreous shell but differs in being "higher and heavier" (Gardner, 1916). It is considered by Gardner to be a "northern race". When the complex of characters is considered the difference in H/L ratio may not be of specific rank. A statistical study may show percrassa and slackiana to be conspecific, as suggested by Gabb (1876), or the difference, if any, to be of subspecific rank only. The divergence of opinion in the placement of some specimens and the reports (Weller, 1907, and others) of percrassa from Maryland-New Jersey, even if they are based on distorted steinkerns, tend to support the first interpretation (see also Weller, 1907, p. 371).

NUCULANA

Author. Link, 1807, p. 155.

Subgenus NUCULANA sensu stricto

Type Species. By monotypy, Arca rostrata Gmelin (1791, p. 3308, \pm A. rostrata Chemnitz 1784, p. 206, P1. 55, figs. 550, 551, which is invalid), Recent, Europe.

Nuculana (Nuculana) grandensis Speden, new species (Plate 2, figs. 12-15)

ETYMOLOGY. From Grand River, South Dakota.

Description. Moderately small, specimens 10.2 to 27.1 mm long, equivalve, inequilateral, compressed, posterior margin with narrow gape. Shape narrow rectangular, posterior end very attenuated, tapering and curving dorsally. Dimensions rather consistent; height, anterior length, and width, respectively, 27.7 to 39.6 (N = 9, μ = 32.7%), 23.1 to 29.2 (N = 9, μ = 26.2%) and 7.7 to 12.6 (N = 6, μ = 10.1%) percent of length. Posterior dorsal margin concave, forms an obtuse angle of about 140 to 170 degrees with convex anterior dorsal margin, anterodorsal margin rounded, anteroventral margin truncated or with a sinuosity, ventral margin convex anteriorly and slightly concave posteriorly, posterior margin convex or sinuous. Umbones insignificant, apparently prosogyrous.

Shell ornamented with irregular fine concentric costae and depressions, with fine growth striae, and sometimes with irregular, shallow, narrow, flat-floored radial grooves anterior to the umbones and posteriorly above a line joining the umbone and the posteroventral extremity. Hinge line about 70 percent of length, taxodont with approximately two to two-and-a-half times more posterior teeth than anterior teeth (42 posterior and 19 anterior teeth on a specimen 16.3 mm long). Teeth concave toward the extremities, interlocking with an angular keel on the convex side and a corresponding groove on the concave side, increase in size toward the extremities, markedly on the anterior segment,

segments separated by a small, shallow, internal triangular resilifer.

Muscle insertion areas weakly impressed. Adductor area unequal, situated under ends of hinge line, posterior insertion area small, rectangular, its long axis parallel to hinge line, the anterior three to four times larger, subquadrangular, its long axis perpendicular to hinge line. Pedal scars unknown. Pallial line with a small U-shaped sinus situated in dorsal half of height, the underlying pallial-line prolongation equally wide and with a rounded posterior end. Ostracum 0.2 to 0.4 mm thick, of three layers. A thin outer prismatic layer, a thick middle lamellar layer and a very thin inner nacreous film.

Types. Holotype YPM 23985 (Pl. 23, fig. 6), a left valve and matching external mould, L = 20.7, H = 6.8, $\frac{1}{2}$ W = 0.8, AL = 5.7 mm, from the *Nucula* layer, Trail City Member, Loc. 25, A289, Grand River, near Bullhead, South Dakota; and 29 paratypes: YPM 23982-84, 24503-28.

Discussion. Most of the specimens from Locality 25, Bullhead are crushed and distorted to varying degrees by compaction. The figures for inflation quoted above give an order of magnitude only. Measurements on growth lines of a specimen from A298 indicate that the posterior attentuation increases with growth. The percentage of anterior length to length decreased from 44.8 for a length of 1.0 mm to 33.7 for a length of 3.3 mm, and then decreased gradually to 25.5 at the final length of 10.2 mm. The other proportions remained approximately constant. This pattern is also evident on other specimens. No trace was seen of outer ligament sockets characteristic of the family Nuculanidae.

MATERIAL. 36 specimens as steinkerns and with shell. The species is represented by 17 specimens from the *Nucula* concretion layer above the *Protocardia-Oxytoma* Assemblage Zone, Trail City Member, Loc. 25, and by 15 specimens from seven localities in the Timber Lake Member.

OCCURRENCE. Rarely more than a single valve per concretion. Four single valves were obtained from A457, Loc. 210, Timber Lake Member, and two or three specimens were collected from some concretions at Loc. 25. Because of the paucity of specimens and

the dominance of disarticulated valves little can be said about possible preferred environments. It may be significant that almost half of the specimens come from Loc. 25 where the only two articulated specimens were collected and where the species is a codominant with *Nucula percrassa* in an assemblage dominated by protobranchs.

Comparisons. Nuculana (N.) grandensis, littlii (Gardner, 1916), and stephensoni Richards (1958) belong to a group of long, compressed and virtually smooth Nuculana species. Nuculana stephensoni has a higher and more rounded anterior end, a more arched anterior hinge segment, a greater height to length ratio, a stronger umbonal to posteroventral angulation, and stronger ornamentation with no radial striae. The posterior angulation and concave dorsal margin are very strong on the specimen figured by Whitfield (1885, Pl. 11, figs. 14, 15). N. littlii is more rectangular and the dorsal margin behind the umbones is straighter.

Subgenus JUPITERIA

Author. Bellardi, 1875, p. 20.

Type Species. By subsequent designation of Dall, 1898, p. 579, Nucula concava Bronn (1831, p. 618), Pliocene, Italy.

Discussion. The bluntly pointed posterior end and lack of dorsal angulations and sulci exclude N. scitula, described below, from Saccella Woodring and Lembulus Risso. Nuculana scitula differs from the subgenus Jupiteria, in which it is here classed, by its more elongated posterior end and its stronger sculpture which cuts across growth increments at a low angle.

Nuculana (Jupiteria) scitula (Meek & Hayden) (Plate 2, figs. 16–21; Plate 3, figs. 1–6)

Nucula scitula Meek & Hayden, 1856a, p. 84.

Leda scitula (Meek & Hayden). Meek & Hayden, 1860a, p. 185.

Leda (Yoldia) scitula (Meek & Hayden). Meek & Hayden, 1860b, p. 428.

Yoldia scitula (Meek & Hayden). Meek, 1876, p. 110, Pl. 28, fig. 9. Whiteaves, 1885, p. 38, Pl. 5, fig. 2. Stanton, 1920, p. 21, Pl. 1, figs. 9 (= type specimen) and 10.

Nuculana bisulcata (Meek & Hayden). Whitfield, 1880, p. 407, Pl. 11, fig. 7.

[?] Yoldia thomi Stanton, 1920, p. 21, Pl. 1, figs. 12a-c.

[?]Nuculana thomi (Stanton). Cvancara, 1966, p. 301, Pl. 1, figs. 22-24.

[?]Yoldia cupressensis Landes, 1940, p. 134, Pl. 1, figs. 7, 8.

[?] Neilonella evansi (Meek & Hayden). Cvancara, 1966, p. 297, Pl. 1, figs. 13-17.

Description. Small, specimens 2.8 to 10.6 mm long, equivalve, inequilateral, compressed to strongly inflated, posterior margin narrow with a small gape. Shape variable, tapers posteriorly or slightly rostrate. Height, width and anterior length, respectively, 47 to 71.8 (N = 134, μ = 59.4%), 22.6 to 60.6 (N = 134, μ = 38.4%) and 31.8 to 48.7 (N = 134, μ = 40.2%) percent of length. Posterior dorsal margin straight, anterior dorsal margin slightly convex, anterodorsal margin convex, anteroventral margin rounded or weakly sinuous, posteroventral margin either short, sinuous in younger stages and straight in adult, and continuing into a long convex ventral margin in tapering specimens, or long, straight to slightly sinuous and continuing into a short rounded ventral margin in rostrate specimens. Umbones vary in prominence, strong and swollen in some, opisthogyrous. Posterodorsal margin of valve with a broad groove of variable prominence, flattens and fades posteriorly, widest on rostrate specimens, bounded by an umbonal to posterodorsal extremity ridge of variable strength, frequently strong and incurving. Anterodorsal

margin with a similar groove on posterior half, bounded by an umbonal ridge of vari-

able strength, which fades anteriorly.

Ornamentation variable, characterized by strong concentric grooves and costae with dorsally pointing crests and longer ventral slopes and, rarely, narrow round-topped ridges. Costae added mostly along central two thirds of ventral margin, both grooves and costae sometimes marked by faint growth striae. Anterior and posterior ends of shell often with growth striae or occasional costae only, or a ray-shaped zone lacking costae may interrupt the concentric costate pattern along axes extending from the umbone to the posteroventral and anteroventral angulations. Faint microscopic radial striae sometimes present, most obvious on smooth areas. Dorsal areas internal to umbonal ridges lack concentric costae. Strong growth corrugations sometimes present. Prodissoconch small, smooth or with fine concentric striae.

Hinge line about four fifths of length, taxodont, anterior segment with 14 to 17 teeth for specimens 7.0 to 7.5 mm long, 2 to 3 less than on posterior segment. Larger specimens have 3 to 5 more teeth in the posterior than in the anterior segment (24 posterior and 19 anterior teeth on a specimen 9.2 mm long). Teeth concave toward the resilifer, strongly interlocking with a keel on the convex side and a corresponding groove on the concave side. Ligament "separated", with an internal triangular resilifer that separates the teeth and an external ligament set in anterior and posterior grooves. External ligament one quarter to one sixth of length of shell, the anterior segment one half to three quarters of length of posterior segment. Both internal resilifer and external grooves extremely variable in dimensions.

Muscle insertion areas weakly impressed. Adductor muscle insertions strongly unequal, situated under ends of hinge. Anterior about four to five times larger than posterior adductor, subquadrangular, its long axis inclined at 35 to 40 degrees to the long axis of shell, bilobate, anterior margin convex, posterior margin concave or straight. Posterior adductor subrectangular, long axis parallel to hinge line, anterior end bilobate, posterior margin convex. Posterior pedal insertion situated close to base of teeth, very narrow and elongate, extends from above anterior end of posterior adductor two thirds of the way to the resilifer. Three anterior suboval pedal insertion areas; one (protractor) above and just posterior to anterior adductor scar, two others (retractors) situated about halfway between anterior adductor and resilifer, discrete, the posterior larger and possibly composite. Pallial sinus U-shaped, of variable depth, its axis parallel to length axis, the end of posteroventral prolongation rounded. Pallial line joins either the ventral or dorsal lobes of the anterior end of the posterior adductor scar, and always joins the ventral extremity of the anterior adductor scar.

Ostracum 0.1 to 0.4 mm thick, of three layers. A thin outer prismatic layer, a thick middle lamellar layer and a thin inner nacreous film.

Types. Lectotype of Nucula scitula, USNM 302, by subsequent designation of Meek (1876, in caption to Pl. 28, fig. 9), a two-valved specimen, L = 10.2, H = 5.6, ½ W = 2.4, AL = 3.1 mm, figured by Meek and also by Stanton (1920, Pl. 1, fig. 9). Type locality: Long Lake, North Dakota. Stratigraphic position: Fox Hills Formation, Timber Lake Member equivalents. Holotype of Yoldia thomi, USNM 32388, designated and figured by Stanton (1920, Pl. 1, figs. 12a-c), a left valve shell, L = 12.8, H = 7.8, ½ W = 3.1, AL = 5.1 mm. Type locality: Cannonball River near Kayser, North Dakota. Stratigraphic position: Cannonball Formation, Paleocene. Meek's figure of scitula is idealized, and the only positive evidence that it is the type is a label and Stanton's label and figure.

Types held at YPM are: hypotypes YPM 23963-70, 24474-75; and 24476.

Discussion. Many of the specimens are pitted and worn in the umbonal region. Only four of the 635 counted specimens were bored. The concentric costation, although characteristic of the species, is extremely variable in pattern and strength. On some specimens the cross-sectional shape of the costae differs on each valve and over different parts of one valve. The intersection of the costae with fine growth striae is characteristic.

The most marked shape variations are the tendency to rostration and the degree of inflation. Rostrate specimens are present in certain concretions in all assemblage zones, but qualitative observations suggest that they are more numerous in the Timber Lake Member and in sand beds as at Locality 92 (A920; Pl. 2, fig. 19). A qualitative observation that shelled specimens of scitula from individual concretions at localities in the Timber Lake Member are consistently more inflated than those in samples from concretions in assemblage zones of the Trail City Member was confirmed by the use of the Wilcoxon distribution-free two-sample test (Bradley, 1960, p. 137-140). The tests were initially based on measurements of specimens with shell, but the inclusion of data from steinkerns did not alter the result. Samples of four or more specimens were tested and the results are presented in Table 1. The results show that the inflation of samples from individual concretions of various assemblage zones in the Timber Lake Member, and of a sample from a concretion from the Protocardia-Oxytoma Assemblage Zone at Loc. 102 is significant at the 95 percent probability level from that of samples from individual concretions of the Lower nicolleti and Limopsis-Pseudoptera assemblage zones. Testing of samples from individual concretions of one locality or from one assemblage zone gave a nonsignificant result in every case. The muddy fine-grained sandstone of the Timber Lake Member and of the Protocardia-Oxytoma at Loc. 102 is distinctly coarser grained than the silty mudstone of the assemblage zones lower in the Trail City Member. Thus there is a correlation of greater inflation with coarser sediment, and so habitat, as shown for Nucula species by Allen (1954).

Many specimens have ligament material preserved in the external sockets (Pl. 2, fig. 21). Qualitative observations suggest that the external ligament is less well developed and the internal ligament more strongly developed on rostrate than on nonrostrate specimens. Recent species of "Leda" (= Nuculana) have identical pedal musculation insertions (Heath, 1937).

MATERIAL. 2027 specimens with shell or as steinkerns. Incompleteness and lack of shell is due mostly to extraction. The stratigraphic distribution of the species is presented in Figure 4.

Occurrence. Mostly less than 10 specimens per concretion, but some concretions in any assemblage zone may have more than 10 and as many as 250. Large numbers occur most commonly in concretions from the Limopsis-Pseudoptera Assemblage Zone, as at Locs. 242 and 191, the Timber Lake Member at 60 and 90, the Cucullaea Assemblage Zone of the Irish Creek lithofacies at 73 and 100. In the Trail City Member Nuculana scitula is a codominant in assemblages with Malletia evansi in the Protocardia-Oxytoma Assemblage Zone at Loc. 102, and in the Timber Lake Member with Protocardia and Phelopteria at Loc. 60, with Discoscaphites, Nucula and Malletia and with Discoscaphites, Malletia and Protocardia at Loc. 90. Where relatively abundant, especially at Loc. 102, the species is usually associated with common to abundant plant remains.

The number of articulated specimens equals or exceeds the number of disarticulated in 31 of 63 concretions sampled in detail. This, the excellent preservation, the paucity of broken specimens, and the fact that the ratio of articulated to disarticulated specimens is greater than one for all assemblage zones and is 1.20:1 for all specimens indicate that transportation has been slight. The species seems to be rather tolerant of lithofacies. It possibly prefers an admixture of sand and mud as in the Timber Lake Member and an abundance of organic matter.

Comparisons. Although crushed, the lectotype of *Nuculana bisulcata* (Meek & Hayden; USNM 1948, L = 7.6, H = 4.4, AL = 3.1 mm) is very rostrate with a pointed posterior end and strong umbonal to posterodorsal keels bordering a depressed posterodorsal area, which has a second strong keel delimiting a wide escutcheon. It represents a distinct species.

The specimen (USNM 12265) from the Pierre Shale of the Black Hills classed by Whitfield (1880) in N. bisulcata is a scitula as interpreted here.

Table 1. Wilcoxon distribution-free two-sample test on inflation (W) of samples of Nuculana (J.) scitula from different members and assemblage zones. Scores m + n are ranked and the smaller sample summed (Rm). Critical values for a two-tailed test at the 95% level of significance are tabled by Owen (1962).

CAZ	= Cucullaea Assemblage Zone	POAZ = Protocardia-Oxytoma Assemblage Zone				
LNAZ	 Irish Creek lithofacies Lower nicolleti Assemblage Zone Limopsis-Pseudoptera Assemblage Zone 	TCM = Trail City Member TLM = Timber Lake Member * = Significant at the 95% level				
	Mombor Loc An	umbor m n Dm				

Member	Loc.	A-number	m	n	Rm
1. TCM, LPAZ TLM	228 90	1120 789	13	17	114*
2. TCM, LPAZ TLM	228 90	1120 788	5	13	80*
3. TCM, LPAZ TLM	228 90	1120 792	4	13	58*
4. TCM, LPAZ TLM	228 90	1120 793	6	13	83*
5. TCM, LPAZ ICL, CAZ	228 92	1120 920	8	13	138*
6. TCM, LPAZ TLM	228 227	1120 776	6	13	88*
7. TCM, LPAZ TLM	228 60	1120 504	6	13	106*
8. TCM, LPAZ ICL, CAZ	228 210	1120 466	5	13	78*
9. TCM, LPAZ ICL, CAZ	228 73	1120 654	6	13	97*
10. TCM, LPAZ TCM, POAZ	228 102	1120 981	13	14	113*
11. TCM, LPAZ TCM, LPAZ	228 191	1120 561	9	13	94
12. TCM, LPAZ TCM, LPAZ	228 242	1120 1063	6	13	67
13. TCM, LPAZ TCM, LNAZ	228 248	1120 1099	4	13	46
14. TCM, POAZ TLM	102 90	981 789	14	17	183
15. TLM ICL, CAZ	90 73	789 654	6	17	66

Specimens from the Cannonball Formation classed by Cvancara (1966) in "Neilonella evansi (Meek & Hayden)?" resemble specimens of scitula from the type Fox Hills in all external respects but appear to have a markedly smaller internal resilifer. This should be checked carefully as some of the nonrostrate Fox Hills specimens have a very small, barely visible internal resilifer (Pl. 3, fig. 4). Dr. Cvancara and I confused the taxa we were discussing by correspondence (Cvancara, 1966, p. 298). I was referring to Malletia evansi (Meek & Hayden) (see below), and he to specimens closely resembling the Fox Hills Nuculana scitula.

The type specimens of Yoldia thomi Stanton (1920; USNM 32388) and those figured by Cvancara (1966) are similar in shape and ornament to some of the more smooth and less rostrate specimens of scitula in the Fox Hills collections, but tend to have more medially placed umbones and to have weaker ornament over the entire valve. Biometric studies may show it to represent a younger part of the scitula lineage and to be a distinct subspecies or species.

Population studies are required to clarify the relationship of scitula to many closely similar species described from Gulf and Atlantic Coastal Plains sequences. Stephenson

(1941) described at least three species closely resembling scitula.

YOLDIA

Author. Möller, 1842, p. 91.

Type Species. By the Plenary Powers of The International Commission of Zoological Nomenclature, Opinion 736 (Bull. Zool. Nomenclature, 1966, v. 23, p. 33), Yoldia hyperborea Torell (1859, p. 149, Pl. 2, figs. 6a, b), Recent, in Boreal seas.

Yoldia lacrima Speden, new species (Plate 3, figs. 7-10)

ETYMOLOGY. From lacrima (latin), pertaining to the tear-shaped form.

Description. Small, specimens 5 to 24 mm long, equivalve, inequilateral, compressed, shaped like a teardrop, with the posterior end pointed and the posterior margin with a slight gape. Shape rather consistent. Height, width and anterior length, respectively, 39.3 to 50 (N = 8, μ = 46.9%), 13.0 to 19.6 (N = 8, μ = 16%) and 38.0 to 44.2 (N = 8, μ = 42.8%) percent of length. Maximum height at umbone. Posterior dorsal margin straight, becomes convex posteriorly and continues into a rounded posterior margin. Anterior dorsal margin straight, continues to a convex anterodorsal margin. Anteroventral margin distinctly sinuous, posteroventral margin sinuous or straight, ventral margin gently convex. Umbones distinct, apparently opisthogyrous. Rows of dental pit markings visible externally along anterior and posterior dorsal margins of valves.

Shell with a glossy surface, ornamented by fine growth striae only. Hinge about two thirds of length, taxodont, posterior and anterior segments separated by a wide, shallow resilifer, posterior segment with one or two more teeth than anterior on small specimens, but with one third more on large specimens (32 posterior and 24 anterior on a specimen 13.8 mm long, YPM 23988), teeth concave toward the extremities with a very prominent

keel on convex side and corresponding socket on concave side.

Adductor insertion areas unequal, weakly impressed, the anterior suboval, larger than posterior, under anterior end of hinge, its long axis perpendicular to length of shell. Posterior subrectangular, its long axis parallel to dorsal margin, situated under and partly behind posterior end of hinge. Anterior pedal retractor insertion small, oval, close to posterodorsal margin of adductor. Posterior pedal insertion linear-subrectangular, under hinge, extending from above adductor for one third of distance toward umbones. Pallial sinus deep, U-shaped, with a narrow posterior ventral prolongation. Ostracum very thin, of three layers. A thin outer prismatic layer, a thick middle lamellar layer and an inner nacreous film.

Types. Holotype, YPM 23988, a two-valved closed specimen with some shell (Pl. 3, fig. 8), only the left valve exposed, and matching external mould, L=13.8, H=6.5, $\frac{1}{2}$ W = 0.9, AL = 6.0 mm, Lower *nicolleti* Assemblage Zone, Trail City Member, and 16 paratypes, YPM 23986-87, 24743, 24529-41.

MATERIAL. 19 specimens as steinkerns and with shell. Several are incomplete due to extraction. All but the largest specimen (from Loc. 56, A441, Cymbophora-Tellinimera Assemblage Zone) from or below the Limopsis-Pseudoptera Assemblage Zone, Trail City Member.

Occurrence. Mostly as a single valve per concretion. Three concretions had two or three specimens. Four articulated specimens are included in the total of 19. Although extremely rare and from geographically widely separated localities, the species may have preferred the environments represented by the silty-mudstone facies of the Trail City Member.

Yoldia rectangularis Speden, new species (Plate 3, figs. 11-14)

ETYMOLOGY. Referring to the distinctive compressed rectangular shape.

Description. Small, length of specimens 6.6 to 19.1 mm, equivalve, inequilateral, compressed. Shape subrectangular, with a slight posterior taper, little variation. Height, width and anterior length, respectively, 41.9 to 47.2 (N = 5, μ = 45.4%), 8.4 to 13.6 (N = 5, μ = 10.9%) and 31.8 to 35.9 (N = 5, μ = 34.2%) percent of length. Dorsal margin straight, anterior and posterior margins rounded with a truncation or slight sinuosity on ventral half, ventral margin very slightly convex. Umbones not prominent, apparently opisthogyrous. Rows of dental pit markings visible for a short distance from the umbones on smallest and thinnest shelled specimens.

Shell ornamented by fine growth striae and irregular concentric growth corrugations, with a zone of fine radial grooves and costae extending from the umbone to the anteroventral margin, and generally with microscopic radial striae over the anterior two thirds of the shell. Hinge about three quarters (71 to 75% for three measurements) of length, very narrow, comprising about 5 percent of height of shell, taxodont. Anterior and posterior hinge segments diverge slightly from a small triangular resilifer situated under umbones, posterior segment with two to two-and-a-half times as many teeth as anterior. Teeth minute, increase in size and are concave toward the extremities, with a more rapid increase in size on the anterior segment. Teeth strongly interlocking with a keel on convex side and a corresponding socket on concave side.

Adductor insertion areas situated under ends of hinge line, large, subequal. Posterior insertion subrectangular, elongated, tapering slightly anteriorly, long axis parallel to hinge line. Anterior subtrapezoidal, long axis perpendicular to hinge line. Pedal insertions unknown. Pallial sinus U-shaped, shallow, situated in dorsal two thirds of height. Posterior end of pallial line joins anteroventral extremity of posterior adductor scar.

Ostracum very thin, of three layers. A thin outer prismatic layer, a thick middle lamellar layer and an inner nacreous film.

Types. Holotype, YPM 23992, a left valve and matching external mould, incomplete ventrally, L = 20.6, H = 8.0, $\frac{1}{2}$ W = 0.8, AL = 6.4 mm, from Loc. 88, A771, abyssinus concretions, Timber Lake Member, and 15 paratypes, YPM 23989–91, 24542–53.

Discussion. The fragility of the shell is reflected in the fact that six of the 18 specimens were broken before or during transport, and that seven (one additional specimen) show crushing which may have occurred simultaneously with the breakage, be due to compaction, or both. One specimen was definitely crushed by compaction only. This breakage and crushing suggests that the inflation data given above may be a minimum range. A fracture across a dental socket shows that there is no "horny process" at the end of the socket as in the case of the *Nucula* species described by Trueman (1954). The row of "markings" is probably due to the thinness of the shell. Traces of fine radial striae and

corrugations, wider than those on the external surface, are present on the anterior end of several steinkerns. Ligament material is preserved in the anterior and posterior segments of the external part of the "separated" ligament on one specimen (YPM 24553). The anterior part of the external ligament is approximately one quarter as long as the posterior.

MATERIAL. Eighteen specimens as steinkerns, with and without external moulds and some shell, mostly incomplete due to breakage before or during deposition, or during extraction.

Occurrence. As single specimens in all concretions, except for one (A428) from Loc. 53 which contained five single valves. The ratio of disarticulated to articulated valves is 2:1. This and the high percentage (50%) of broken specimens indicate transportation. Yet the ligament is so small relative to the size of the shell that the occurrence of articulated specimens implies moderate or little transportation. Ten of the specimens are from concretions from the Timber Lake Member. The remainder came from the Lower nicolleti Assemblage Zone, Trail City Member.

COMPARISON. The subrectangular shape and the straight dorsal margin of rectangularis are more characteristic of Malletia than of Yoldia in which the species belongs by its possession of a separated ligament. It cannot be confused with any other species described from Western Interior sequences.

MALLETIA

Author. Desmoulins, 1832, p. 85.

Type Species. By monotypy, Malletia chilensis Desmoulins (1832, p. 90), Recent, Chile.

Malletia evansi (Meek & Hayden) (Plate 3, figs. 15–19; Plate 4, figs. 1–7)

Nucula evansi Meek & Hayden, 1856a, p. 84.

Leda evansi (Meek & Hayden). Meek & Hayden, 1860a, p. 185.

Leda (Yoldia) evansi (Meek & Hayden). Meek & Hayden, 1860b, p. 429.

Yoldia evansi (Meek & Hayden). Meek, 1876, p. 111, Pl. 28, figs. 10a, b, c. Whitfield, 1880, p. 409, Pl. 11, figs. 1, 2. Whiteaves, 1885, p. 38.

[?]Yoldia dowlingi Landes, 1940, p. 133, Pl. 1, figs. 9, 10.

Description. Shape elongate subquadrangular, specimens 3.6 to 18.5 mm long, equivalve, inequilateral, compressed, posterior margin with a narrow gape along dorsal half. Shape variable; height 40 to 61.1 (N = 100, μ = 49.3%), width 12.2 to 29.1 (N = 100, μ = 20.9%) and anterior length 29.1 to 44.2 (N = 100, μ = 36.4%) percent of length. Posterior dorsal margin straight, anterior dorsal margin straight to weakly convex, anterodorsal margin rounded, anteroventral margin convex or with a slight sinuosity, ventral margin mostly slightly convex, rarely straight or concave, posterior ventral margin sinuous to convex and longer than the rounded posterodorsal margin. Umbones not prominent, opisthogyrous. Behind the umbones is a prominent, flat, dorsal triangular platform, extending three quarters of the posterior length of the shell, bordered externally for the anterior half of its length by a sharp incurving ridge, and internally the commissure margin is sometimes reflexed upward. Anterior to umbones a less prominent triangular area is defined by umbonal ridges that fade anteriorly.

Shell almost smooth, with faint growth striae, rarely with broad, low growth corrugations, many with color banding. Small and thin-shelled specimens show dental socket

markings close to the dorsal commissure. Hinge line about four fifths of length, taxodont. Anterior segment with about three fifths the number of teeth of the posterior segment. Teeth concave toward extremities, decrease in size in both directions from center of segments, strongly interlocking with a flat-sided keel on convex side and a flat-sided socket on concave side (Pl. 4, fig. 5). Teeth continuous over center of hinge near dorsal margin, leaving a small triangular platform (lacking a resilifer pit) below. Central small teeth variable in size and shape, a large tooth sometimes present. Ligament external in narrow deep grooves anterior and posterior to umbones, delimited ventrally by the teeth, about one fifth of length, the anterior segment half as long as posterior.

Muscle insertion areas faint, slightly impressed in larger thick-shelled specimens. Adductor insertions unequal, situated under the ends of hinge line. Anterior insertion larger, subquadrangular, broadest ventrally, sometimes with a sinuous posterior and/or ventral margin, longest axis at small angle to the vertical. Posterior insertion more strongly impressed, about one-half to two-thirds size of anterior, narrow rectangular, long axis approximately parallel to dorsal margin. Posterior pedal insertion area situated close to base of teeth, very narrow and elongated, extends from above posterior adductor two thirds the distance to umbones. Anterior pedal insertions very indefinite, apparently only two impressions, a large subquadrangular one, constricted about middle of height and tending to be bilobate, long axis approximately perpendicular to hinge, situated about halfway between umbone and anterior adductor insertion area, and just posterior and slightly above is a small, more strongly impressed oval insertion (anterior pedal retractor). An elliptical dorsomedian insertion area (the musculus protractor pedis posterior of Stoll, 1939) is sometimes visible.

Pallial line with a deep U-shaped sinus, variable in shape and becoming more V-shaped when posterior end of valve tapers, the posteroventral prolongation of the pallial line narrow, tapering, often curved dorsally at posterior end. Pallial line joins posterior adductor at or near its anteroventral end.

Ostracum 0.2 to 0.6 mm thick, of three layers. A thin outer prismatic layer, a thick middle lamellar layer and a very thin inner nacreous film.

Types. Lectotype of *Nucula evansi*, USNM 307, by subsequent designation of Meek (1876, in caption to Pl. 28, fig. 10b), a well-preserved left valve, L = 18.4, H = 7.4, $\frac{1}{2}$ W = 2.7, AL = 6.2 mm. Type locality: Moreau River, South Dakota. Stratigraphic position: Fox Hills Formation.

Also in the collection USNM 307 is the original of Meek's Plate 28, figure 10a, L = 14.4, H = 6.2, W = 5.2, AL = 4.9 mm. The associated fossils and lithology indicate that the specimens were collected from the Timber Lake Member.

Types held at YPM are: hypotypes YPM 23971-81.

Discussion. Many specimens have worn and pitted umbones (see Stoll, 1939, Pl. 1), which is compatible with the life position when the long axis is approximately parallel to the substrate surface (Yonge, 1939, fig. 6). The erosion of the umbonal region often contrasts with the excellent preservation of the remainder of the shell and with the presence of ligament material in the ligament sockets (Pl. 3, fig. 15). At several localities (Locs. 90, 100, 110) as many as 25 to 50 percent of the articulated specimens retained ligament material. Several specimens have fine borings. The maximum inflation occurs below the umbones. On some specimens a faint sulcus, situated below the umbones and at about half the height of the shell, results in two bulges. The sinuosity of the posteroventral margin is most prominent on moderate-size specimens but disappears with increasing size (Pl. 25, fig. 8; see also Stoll, 1939, Pl. 1). The pallial sinus on the specimen figured by Meek (1876, Pl. 28, fig. 10c) is idealized, being drawn too deep and with the position of maximum depth too close to the dorsal margin.

The description of the weakly bilobed and larger anterior pedal insertion area is based on one specimen. The shape may be the result of coalescence of two pedal muscles, possibly the protractors. If this is true and the pattern is consistent, it contrasts with the three linearly arranged insertions described and figured (Stoll, 1939, fig. 40) for the re-

cent species Malletia gigantea (Smith) and may be of evolutionary or functional significance.

MATERIAL. 1629 specimens as steinkerns and with shell. The incompleteness of the specimens and lack of shell is mostly due to extraction. Only three specimens were broken during or before transportation and deposition.

Occurrence. Mostly as a few specimens per concretion in all assemblage zones. Single valves dominate, and the ratio of disarticulated to articulated valves is about 3:1 within all assemblage zones. Articulated specimens are more numerous where the species is abundant and single valves where it is represented by less than five specimens. The specimens with articulated valves all gaped ventrally, in some cases only slightly. Considering the large number of Limopsis-Pseudoptera and Protocardia-Oxytoma assemblage zone concretions broken down, the qualitative field observation that M. evansi is most numerous in the Lower nicolleti Assemblage Zone and in Timber Lake Member is supported by the counts. In the Timber Lake Member evansi is particularly abundant in concretions in and below the Sphenodiscus concretion layer at Loc. 90, where 133 specimens were collected from one concretion (A788), and also at Loc. 100, Irish Creek lithofacies, Cucullaea Assemblage Zone, in float concretions. Where more than 15 specimens were collected from a concretion (25 at 17 localities) there is also normally a high content of large or finely comminuted plant fragments and sometimes bored wood stems. Plant material is always abundant when M. evansi is a codominant in associations (Pl. 41, fig. 2; A788, Loc. 90). Malletia evansi is never dominant in any association but is frequently codominant with other infaunal species, particularly Nucula sp., Nuculana scitula, Protocardia and Cucullaea.

Comparisons. Some specimens of evansi tend to have a pointed posterior end somewhat resembling that of dowlingi Landes, and the two species may prove to be conspecific. Nuculana longifrons (Conrad) from Upper Cretaceous Atlantic and Gulf Coastal Plains sequences has very similar external shape. The specimen figured by Wade (1926, Pl. 8, fig. 13) clearly lacks an internal resilifer and is a Malletia. Stanton's (1920) specimen (USNM 32387) from the Cannonball Formation is indeterminable. Its inflation and shape suggests placement under Nuculana scitula.

SOLEMYACEA

SOLEMYA sensu stricto

Author. Lamarck, 1818, p. 488.

Type Species. By subsequent designation of Children (1823, p. 300), Tellina togata Poli (1791, p. 42; = Solemya mediterranea Lamarck, 1818, p. 489), Recent, Mediterranean, Adriatic, Madeira and Senegal.

Solemya subplicata (Meek & Hayden) (Plate 4, figs. 8–10, 12)

Solen subplicatus Meek & Hayden, 1856a, p. 82. Solemya subplicata (Meek & Hayden). Meek, 1864a, p. 11. Meek, 1876, p. 129, Pl. 28, fig. 19. Solenomya subplicata (Meek & Hayden). Quenstedt, 1962, p. 35 (complete synonymy).

Description. Medium-sized, specimens 7.3 to 38 mm long, equivalve, inequilateral. Shape subrectangular and subcylindrical, with maximum height situated about one third

of length from posterior end. Height, width and posterior length, respectively, 32.9 to 43.1 (N = 7, μ = 37.6%), 22.2 to 27.4 (N = 5, μ = 24.8%), and 13.3 to 19.9 (N = 7, μ = 16.7%) percent of length. Umbones insignificant, do not project above dorsal margin. Posterior dorsal margin slightly convex, anterior and posterior ends rounded, ventral margin straight or concave.

Shell ornamented by fine growth lines, often delimiting color bands, and by radial plicae of variable prominence, most distinct antero- and posterodorsally. Plicae corrugate the shell margins, are of variable width, tend to be diffuse and broad laterally and with secondary sulci ventrally. Six to nine plicae at anterior end and five to seven at posterior. A narrow raised welt extends down center of most plicae. Interior of shell with fine radial striae, strongest dorsal to ventral margin of adductor scars. Hinge edentulous. From just behind the beaks a prosoclinal buttress, for supporting the internal part of the ligament, extends ventrally for a short distance. Adductor insertion areas unequal, relatively large. Anterior insertion the larger, subquadrangular, its long axis parallels the dorsal margin. Posterior insertion subtrapezoidal, its long axis approximately parallels the dorsal margin, with a strong buttress along the posterodorsal margin. Pedal insertion areas unknown, pallial line simple.

Ostracum thin, composed of prisms aligned perpendicular to the surface, the prisms combine to form irregular rays extending outward from ridges at center of plicae and

tend to give the impression of a radiating striate ornament.

Types. Lectotype, USNM 449, by subsequent designation of Meek (1876, in caption of Pl. 28, fig. 19; figure idealized), a bivalved gaping specimen, L = c.28, H = c.11.5, posterior length = c.5.5 mm. Type locality: Moreau River, South Dakota. Stratigraphic position: Fox Hills Formation.

Types held at YPM are: hypotypes YPM 23993–96.

Discussion. Contrary to Meek's statement (1876, p. 129) the radial striae are distinct on every reasonably preserved specimen. As he considered the radial "minute, closely-set striae" are due to the prismatic shell structure. Although the umbonal region is poorly preserved the internal ligament support and the remnants of ligament material on one specimen (YPM 23993) suggest that the ligament distribution matches that of the recent S. parkinsoni Smith. Due to incompleteness and the periostracal construction of the ventral margin the measurements are approximations only.

MATERIAL. 27 specimens, including nine bivalved articulated, as steinkerns and with shell.

Occurrence. A single specimen per concretion, except for three (A623, A931, A1073), each with three specimens, and one (A658) with two. The high incidence of broken specimens (24%) and the ratio 1.33:1 of disarticulated to articulated valves reflect transportation and the fragility of the shell, possibly more the latter as the shell surface where preserved is unworn. Twenty-two percent (6) of the specimens are from the Timber Lake Member, the remainder from the Trail City Member.

The species has been recorded from Greenland and Japan (Quenstedt, 1962), but these specimens require careful checking.

Comparison. Solemya bilix White (1881, USNM 893) is smaller, has finer radial ornament, and a stronger more calcified shell.

ARCACEA

LIMOPSIS

Author. Sasso, 1827, p. 476.

Type Species. By monotypy, Arca aurita Brocchi (1814, p. 485), Miocene and Pliocene, Italy, and Recent in North Atlantic Ocean.

Limopsis striatopunctatus Evans & Shumard (Plate 4, figs. 11, 13, 14; Plate 5, figs. 1–11)

Limopsis striato-punctatus Evans & Shumard, 1857, p. 38, Meek, 1876, p. 97.

DESCRIPTION. Small, specimens 3.1 to 18.6 mm long, equivalve, inequilateral, prosocline. Shape extremely variable, subquadrangular to subtrapezoidal and very prosocline (Pl. 4, fig. 13). Height, width and anterior length for N=192, respectively, 76.2 to 100 ($\mu=192$).

87.9%), 45.5 to 75 ($\mu = 56.1\%$) and 28.6 to 49.1 ($\mu = 37\%$) percent of length.

Umbones opisthogyrous, prominent. Cardinal area triangular, its length 33.1 to 63.1 (N = 147, μ = 46.4%) percent of length of shell, ornamented by growth striae parallel to commissure margin, separated into two segments by a triangular ligament pit, the anterior segment 25 to 50 (N = 29, μ = 38.4%) percent of length of cardinal area. Ligament pit variable in form and dimensions, widest at commissure, 14.1 to 47.3 (N = 35, μ = 29.2%) percent of length of cardinal area. Cardinal area bounded laterally by overhanging walls. Ligament pit sometimes with two discrete ligament-bearing plates.

Ornamentation variable, with fine growth striae, impressed concentric grooves and occasional prominent growth depressions. Concentric ornament crossed by fine radial grooves with small pits developed at the point of intersection giving a punctate appearance. Posterodorsal part of disc with 5 to 10 fine radial costae, anterodorsal flank sometimes smooth. Prodissoconch with concentric ornament only, sometimes delimited from main disc of shell by a growth constriction. Internal surface finely pitted and with fine radial costae, strongest ventrally above a smooth and sometimes thickened ventral marginal band.

Hinge curved, narrow to wide, variable in shape and dentition, its length 52.3 to 65.9 (N = 25, μ = 60.2%) percent of length of shell. Prionodont, center of hinge edentulous, 7 to 12 posterior and 7 to 10 anterior teeth, with 1 to 3 more teeth on the posterior segment, rarely with equal numbers or one more tooth on anterior segment. Teeth on anterior segment consistently extend well under ventral margin of ligament pit, but rarely more than one tooth occurs under posterior margin of ligament pit. Teeth at extremities of segments conical, those at ventral extremities sometimes bifid or trifid, those in center L-shaped with a thin upper limb parallel to, and a thick platelike or conical limb perpendicular to hinge margin. Dorsal and ventral surfaces of teeth serrated, serrations most prominent on ventral teeth of larger specimens.

Adductor muscle insertion areas impressed, unequal, the anterior subelliptical, situated under end of hinge line, half the size of posterior, its long axis parallel to hinge line, buttressed posterodorsally with the buttress continuing dorsally into umbone and defining a platform above the scar. Posterior adductor insertion subrectangular, sited below end of hinge at half the height of shell, its long axis perpendicular to margin, divided by a weak ridge into a larger smooth-surfaced posterior part and an anterior punctate-surfaced part of extremely variable size. Pedal muscle insertion areas unequal, the anterior small, under end of hinge, narrow rectangular, its long axis parallel to hinge line, moderately to deeply impressed, the posterior trapezoidal, its long axis parallel to margin, weakly impressed, sited between end of hinge and above posterior adductor scar with which it is sometimes confluent. A narrow linear insertion area extends from the base of the posterior margin of the anterior adductor dorsally along the buttress up into the apex of the umbone. Pallial line simple.

Ostracum of two layers, a thick outer concentric cross-lamellar layer and, above the pallial line, an inner complex cross-lamellar layer that is thickest in the dorsal part of the shell.

Types. The location of Evans and Shumard's specimens is unknown. No holotype has

been figured or designated. Type locality: Moreau and Grand Rivers, South Dakota. Stratigraphic position: Fox Hills Formation. Evans and Shumard's (1857, p. 38) comment that the species occurs in layers "nearly a foot thick" indicates that their collection probably came from *Limopsis-Pseudoptera* Assemblage Zone.

Types held at YPM are: hypotypes YPM 23997-24008.

Discussion. The excellent preservation of this species is indicated by the occurrence of ligament material in the ligament pit of all 31 of the articulated specimens on which the cardinal area was exposed (Pl. 5, fig. 6). The tips of the umbones of most specimens are eroded and pitted.

The striking feature of Limopsis striatopuncatatus is the variability of the major morphological features, the shape (Pl. 4, figs. 11, 13, 14), hinge form and dentition (Pl. 5, figs. 5-8), and ornamentation, shown by specimens from a sample of one concretion. An indication of this variability is given by the spread of percentage valves given in the description above. The ornamentation is relatively the most consistent, yet the distinctive radial grooves and punctate pattern frequently require magnification before being visible, and then may be obvious only on the ventral half of the shell. Scatter diagrams suggest that there is a tendency for the more prosoclinal specimens, those with low height to length ratios, to have a longer hinge line and a longer cardinal area, a distinct trend for specimens with a longer cardinal area to have a wider ligament pit, and a tendency for those with a wider ligament pit to have fewer teeth (Pl. 5, fig. 7). The latter may be explained functionally if the increased size of the ligament pit is correctly interpreted as compensating for the reduced interlocking efficiency of the fewer, and generally smaller, teeth. No relationship between the number of teeth and the size or shape of the shell or the length of the hinge line is indicated by scatter diagrams. The suggested tendencies require confirmation by measurements from a larger number of specimens.

An extreme variation in the form of the ligament pit is shown by one specimen (YPM 24005) which has two protruding liplike platforms on the thin ventral margin instead of the normal one. The ligament has split into two separated growth regions, each buttressed independently. When the valves are articulated and closed the central part of the hinge bordering the ligament pit has a narrow slit for a dorsal extension of the mantle. Heavy callusing, particularly as lumps near adductor muscle insertion areas and in the umbonal region and, rarely, as concentric bands (Pl. 5, fig. 7), is present

on the internal shell surface of many specimens.

The pattern and shape of the muscle insertions closely resemble those of the recent L. multistriata (Forskal; see Pelseneer, 1911, Pl. 1, fig. 10). Limopsis striatopunctatus differs by the apparent absence of an anterior protractor insertion and the presence of a linear insertion extending from the anterior adductor into the umbonal cavity. Specimens of the Recent sulcata (Verrill & Bush) possess a similar faint linear insertion area. This linear insertion may represent the attachment of the musculation of labial palps, which are well developed on multistriata, or a coalescence of pedal, labial palp and visceral muscles.

MATERIAL. About 20,000 specimens as individuals extracted from concretions, in entire representative concretions, and in blocks from concretions.

Occurrence. The species is characteristic of and virtually restricted to Limopsis-Pseudoptera Assemblage Zone. Most concretions in the lower layer are composed purely of or are dominated by Limopsis. It also occurs as a minor component in the overlying Protocardia-Oxytoma Assemblage Zone, particularly in Protocardia associations. Specimens in matrix were observed at two localities (30, 253).

At many localities adjacent monospecific associations of *Limopsis*, in a layer, and separated by only one-and-a-half to three feet are composed of essentially nonoverlapping size-frequency classes (Pl. 5, figs. 9–11). Figure 5 shows an example from Loc. 248 where only one specimen overlaps size-frequency classes of length for adjacent samples A1097 and A1098. These restricted size-frequency assemblages probably are related to groupings

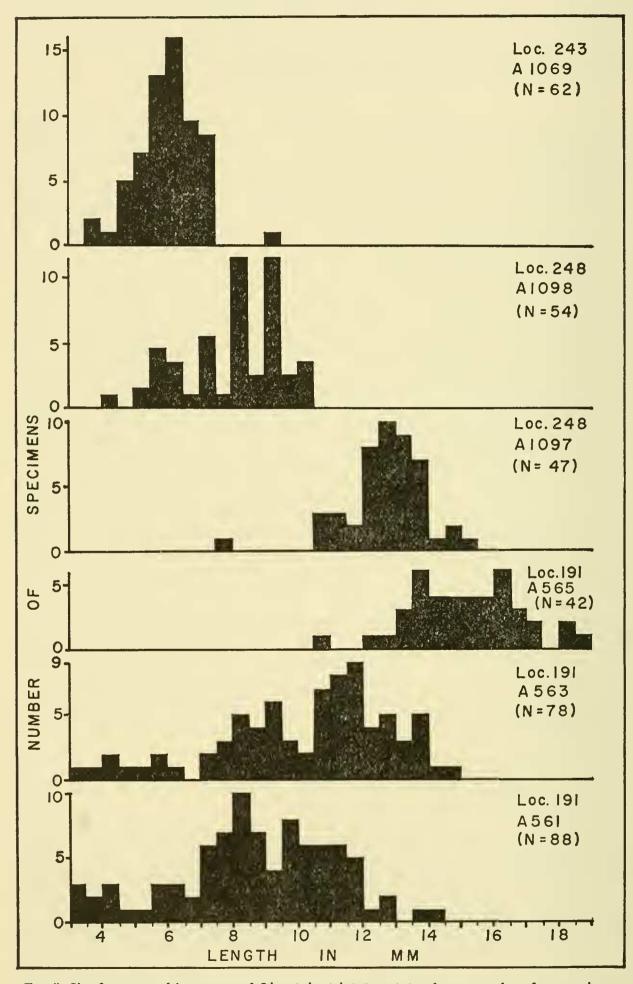


Fig. 5. Size-frequency histograms of Limopsis striatopunctatus from samples of concretions.

of successful spatfalls and are discussed further in the text covering the paleozoological aspects of this study.

COMPARISON. A sample (YPM 23944) of Limopsis parvula (Meek & Hayden) from the "Yellowstone River, Montana", collected by Warren and Hayden and labeled by Meek, shows that parvula is quite distinct. It has a weakly to strongly costate inner shell surface, especially ventrally where the costae end in strong crenules, and fewer and much weaker, generally faintly punctate impressed striae. Ventral crenulations are characteristic of Pectunculina d'Orbigny.

CUCULLAEA

Author. Lamarck, 1801, p. 116.

Type Species. By subsequent designation of Children (1823, p. 318), Arca labiata Solander (1786, p. 185) = Cucullaea auriculifera Lamarck, 1801, p. 116), Recent, Indo-Pacific.

Discussion. Some authors, including Gillet (1924) and Stewart (1930), considered *Idone-arca* Conrad (1862, p. 289), type species *C. vulgaris* Morton, to be a subgenus of *Cucullaea* or a distinct genus. Cox (1940, p. 55) has given good reasons for synonymizing *Idonearca* under *Cucullaea*, and his conclusion is accepted here. The variability of the recent *C. labiata*, discussed by Nicol (1950a), supports this step.

Cucullaea nebrascensis Owen (Plate 6, figs. 1–14; Plate 7, figs. 1–6)

Cucullaea nebrascensis Owen, 1852, p. 582, Pl. 8, figs. 1a, b. Stanton, 1920, p. 22.

Arca (Cucullaea) shumardi Meek & Hayden, 1856a, p. 86.

Arca (Cucullaea) cordata Meek & Hayden, 1856a, p. 86.

Cucullaea shumardi (Meek & Hayden). Meek & Hayden, 1856c, p. 285. Stanton, 1920, p. 22, Pl. 2, figs. la, b.

Cucullaea cordata (Meek & Hayden). Meek & Hayden, 1856c, p. 285.

Cucullaea fibrosa Sowerby. Meek & Hayden, 1860b, p. 428.

Cucullaea (Idonearca) shumardi (Meek & Hayden). Meek, 1876, p. 86-87, Pl. 28, figs. 15a-g; Pl. 29, fig. 4.

Cucullaea (Idonearca) nebrascensis Owen. Meek, 1876, p. 88-89, Pl. 29, figs. 5a,b.

Cucullaea (Idonearca?) cordata (Meek & Hayden). Meek, 1876, p. 89-90, Pl. 29, fig. 6.

Idonearca shumardi (Meek & Hayden). Whitfield, 1880, p. 405, Pl. 11, figs. 8-11.

Description. Large, length of left valves 4.3 to 72.7 mm, inequilateral, generally inequivalve, with length, height and width of right valve, respectively, 96.7 to 100 (N = 50, μ = 98.5%), 93.4 to 99.7 (N = 52, μ = 97.7%) and 92.5 to 103.4 (N = 53, μ = 98.7%) percent of left valve measurements, the inequivalveness mainly along ventral and posteroventral margin, moderately to strongly inflated. Shape extremely variable, subrectangular to subrhomboidal, when sometimes relatively strongly prosocline. Height, anterior length, width and length of dorsal margin of left valve, respectively, 81.4 to 102.5 (N = 96, μ = 88.7%), 34.4 to 50 (N = 97, μ = 43.6%), 23.9 to 44.3 (N = 96, μ = 32.8%) and 44.6 to 82.7 (N = 98, μ = 63.1%) percent of length. Height, anterior length, width and length of dorsal margin of right valve, respectively, 80 to 102.5 (N = 106, μ = 88.6%), 34.1 to 51.6 (N = 119, μ = 43.7%), 25.4 to 46.9 (N = 106, μ = 33.3%) and 53.5 to 83.7 (N = 103, μ = 65.8%) percent of length. Combined width of valves 49.2 to 85.3 percent (N = 52, μ = 65.5%) of length of left valve, and height of umbones above dorsal margin of hinge 11.4 to 18.4 percent (μ = 15.2%) of height for 11 of the largest specimens. Umbones prosogyrous, degree of incurvature and prominence variable, with a faint,

narrow, medial sulcus visible only on small (length less than 10 mm) specimens and less prominent on left valve. Ligament amphidetic, duplivincular. Cardinal area triangular, length 36.4 to 93.2 percent (N = 77, μ = 76%) and 35.9 to 93.7 percent (N = 96, μ = 77.9%) of length of dorsal margin of left and right valve, respectively, and width 7.4 to 18.9 percent (N = 63, μ = 11.6%) and 7.4 to 28.6 percent (N = 91, μ = 12%) of length for left and right valve, respectively, with one to 16 chevron grooves (Fig. 8), crossed by fine striae and grooves that parallel the commissure.

Shell ornamented with weak radial costae that fade ventrally, crossed by concentric growth striae, ridges and depressions that become more prominent ventrally. Multicostate, secondaries and rare tertiaries appear by intercalation and gemmation (rare), costae narrower than interspaces, sharp-topped, wider when crossed by striae. Costae on anterodorsal flank nodose. Primary costae markedly stronger than secondaries or tertiaries, vary in prominence over surface of valve, generally stronger on anterodorsal flank, stronger or more numerous on either valve. Prodissoconch smooth, secondary costae appear at 3 to 4 mm, tertiary at 7 to 11 mm. Valves have 35 to 60 costae at 5 mm height, 48 to 80 at 10 mm, and 54 to 93 on specimens up to 19.3 mm in height. On the right valve a narrow strong costa extends from umbones to meet posterodorsal margin at about two thirds of height, crest of costa plaited by growth striae and ridges, broadens and fades on very large specimens (Pl. 6, fig. 2). Left valve with an indistinct broad costa that meets posterior margin above the costa of right valve. Costa on each valve bordered dorsally and ventrally by faint broad sulci. Costae and sulci give posterodorsal margin a sinuous outline, tending to become alate on large specimens when dorsal sulcus is very strong (Pl. 6, fig. 8).

Table 2. Identification of teeth in Figure 6.

1.	YPM 23882	Loc. 73	A655	16.	YPM 23900	Loc. 92	A920
2.	23883	73	655	17.	23888	73	655
3.	23904	100	973	18.	23889	73	655
4.	23905	100	973	19.	23890	73	655
5.	23884	73	655	20.	23896	92	799
6.	23885	73	655	21.	23891	73	655
7.	23893	73	655	22.	23892	73	655
8.	23886	73	655	23.	23910	37	348
9.	23899	92	920	24.	23897	92	799
10.	23887	73	655	25.	23898	92	799
11.	23908	210	460	26.	23901	92	920
12.	23894	73	658	27.	23907	100	973
13.	23945	100	972	28.	23902	92	920
14.	23895	92	799	29.	23903	92	920
15.	23906	100	973	30.	23909	210	460

Hinge line 59 to 76.5 (N = 11, μ = 65.9%) and 62 to 80.8 (N = 16, μ = 71%) percent of length of left and right valve, respectively, and 92.6 to 108.9 (N = 11, μ = 102.3%) and 89 to 108.6 (N = 16, μ = 99.2%) percent of length of dorsal margin of right and left valve respectively. Dorsal margin of hinge straight, ventral margin arched, hinge thinnest posterior to center. Prionodont, hinge line composed of three segments: anterior and posterior segments with laminar teeth that approximately parallel the dorsal margin at the central end and generally slope ventrally, sometimes strongly, at the posterior and anterior extremities, central ends sometimes weakly to strongly hooked; and a central segment with short platelike teeth steeply inclined or perpendicular to the dorsal margin, and with or without nodular, L-shaped and U-shaped teeth (Table 2 and Fig. 6). Dorsal and ventral surface of laminar teeth are grooved, the serrations at inner end of dorsal two or three laminar teeth become large and strong (Pl. 7, figs. 5, 6) on big (length greater than 30 mm) specimens, forming secondary platelike teeth that may fuse to give diverse shapes. Crest of laminar teeth smooth, more or less concave due to marginal ridges formed by fusion of ends of serrations. Central teeth finely grooved. Anterior segment 25.2 to 45.8 (N = 27, μ = 37.2%), central segment 10.5 to 54.0 (N =

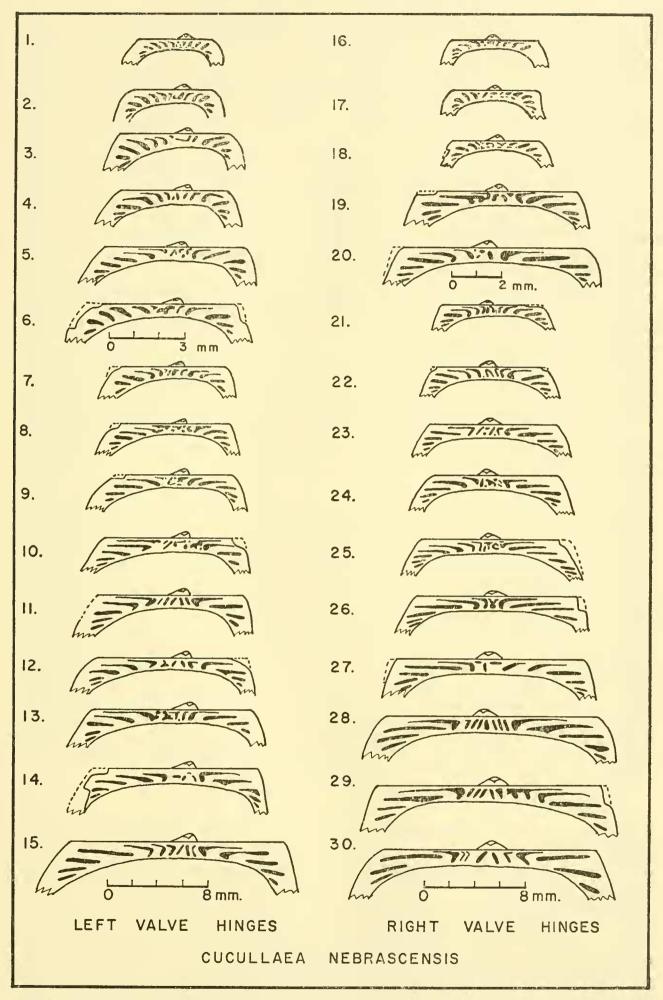


Fig. 6. Arrangement and shape (schematic) of teeth on hinges of small specimens (length of hinge < 20 mm) of Cucullaea nebrascensis Owen. Note how the teeth become less radially arranged and more elongate with growth.

27, $\mu=21.2\%$) and posterior segment 20.8 to 49.3 (N = 27, $\mu=41.7\%$) percent of length of hinge of left valve and, respectively, 28.6 to 46.2 (N = 22, $\mu=38.2\%$), 9.5 to 43.6 (N = 22, $\mu=23.2\%$) and 23.4 to 47.1 (N = 22, $\mu=38.4\%$) percent of length of hinge of right valve. Posterior segment generally the longer for specimens less than 15 mm long, but anterior mostly longer for specimens of greater length. Central segment generally shorter than other two segments for specimens less than 24 mm, of variable proportions for larger specimens when it commonly comprises more than 40 percent of length of hinge.

Adductor insertion areas subequal, the anterior smaller, subtrapezoidal, its long axis directed dorsally. Posterior insertion elongated subtrapezoidal, its long axis directed anterodorsally, anterior half on the ventral end of a prominent platelike buttress that narrows and fades dorsally, becoming indistinct below lower margin of hinge. Pedal insertion areas associated with a narrow pallial band that extends along the ventral margin of hinge and connects the adductor insertions. Anterior pedal insertion elongate oval to irregular, under end of anterior hinge segment. Posterior pedal insertion under and extending most of length of posterior hinge segment, suboval, 10 to 18 times larger than anterior insertion, confluent with posterior adductor at ventral extremity, marked by growth and radial lines. A small, deeply impressed rectangular insertion area is situated well up inside the umbonal cavity above the line of the buttress plate. Pallial line simple, reflexes inward to join ventral extremity of posterior adductor at end of buttress. Inner surface of shell marked by widely spaced thin costae which occur above and are usually distinct only close to pallial line. Inner margin of left valve with thickened border and groove, strongest posterodorsally, for reception of margin of right valve.

Ostracum up to 7.0 mm thick for large specimens, of three layers. A thick outer cross-lamellar layer, a middle thin prismatic myostracum and a moderately thick inner complex cross-lamellar layer.

Types. Lectotype of Cucullaea nebrascensis Owen, USNM 20245, here designated, the original of Plate 7, figure 1a, b of Owen (1852), a left valve, L = 55.6, H = 53.4, 1/9 W = 24.4, AL = 27.6, and length of dorsal margin (DML) = 46.3 mm. Type locality: Fox Hills, between Cheyenne and Moreau Rivers, South Dakota. Stratigraphic position: Fox Hills Formation, probably from the Timber Lake Member. Lectotype of Arca (Cucullaea) cordata Meek & Hayden, USNM 430, by subsequent designation of Meek (1876, in caption to P1. 29, fig. 6a), a bivalved shell, L = 50.6, H = 50.2, W = 44.7, AL = 20.6, DML = 32.3 mm. Type locality: Moreau Trading Post, Moreau River, South Dakota. Stratigraphic position: Fox Hills Formation. Meek's (1876) figure is idealized, the radials being overemphasized. Lectotype of Arca (Cucullaea) shumardi, USNM 443, by subsequent designation of Meek (1876, in caption to P1. 28, fig. 15a), a small (juvenile) bivalved shell, the left valve measurements, L = 16.3, H = 14.0, W = 10.1, AL = 5.8, DML = 10.110.6 mm. Type locality and stratigraphic position: as for cordata. The lectotype is associated in the same collection with large (up to L = 49.1 mm) and small (L = 10.3 mm) specimens some of which resemble cordata and nebrascensis. The associated species and lithology indicate collection from the Timber Lake Member.

Types held at YPM are: hypotypes YPM 23882-23910, 24013, 24659-66.

Discussion. Fossil populations (A655, 799, 920, 973) indicate that *C. nebrascensis* is notable for extreme variation in most factors normally used in systematic studies for differentiation of species, in particular the shape measurements, ornamentation, hinge and cardinal area characteristics. The radial costation is never strong, may be indistinct even on small specimens and is easily destroyed by abrasion during transportation or during life. Pitting of the tip of the umbone is present on many specimens. Ligament material is preserved on most specimens. Inner and outer layers, as described for *Arca* by Owen (1959), are present. An oval rod of dark brown finely crystalline outer ligament extends along the upper commissure margin, branching at intervals to give the chevrons, between which are bands of light brown inner ligament consisting of pearly lamellae (Pl. 7, fig. 3, YPM 24013). The pattern of chevrons is symmetrical on each valve,

but an extra anterior or posterior limb may be inserted between any of the first five chevrons. The apex of the first chevron is situated slightly posterior to the umbone, and for later formed chevrons it tends to migrate posteriorly. The limbs of chevrons are generally straight, may be wavy, and frequently have secondary apices, particularly on the posterior segment. The shapes and proportions of the hinge are diverse. With increasing size the notable trends are the complication of the inner ends of the lamellar teeth by growth of the serrations, the anterior segment becoming mostly longer than the posterior, converse to the situation on small specimens, and the extreme range of width of the central segment for large specimens. When the latter is small few teeth are borne, but large numbers of teeth (10 to 19) generally occur when it is long (Pls. 6, 7).

The occurrence of two marked size groups in the Cucullaea Assemblage Zone along the Moreau River, namely, the essential restriction of large specimens (length greater than 40 mm) to the matrix and of small specimens (length mostly less than 30 mm) characteristically to concretions and shellbeds suggested that they were possibly distinct species perhaps occupying different ecological niches. Qualitative morphological observations tended to support this, for the large specimens generally lacked radial costae, appeared to be more inflated and to possess a longer cardinal area compared to the length of the dorsal margin. Comparison of the mean values, the ranges being much the same, for the ratios of height/length, anterior length/length, cardinal area width/cardinal area length, length of hinge line/length and length of cardinal area, width to length, length of dorsal margin to length, and length of cardinal area to length of dorsal margin showed that the values for samples of small and large specimens were within one to 4 percent, probably within the sample bias, except for the last three ratios which were respectively 5, 8 and 13 percent apart. Construction of graphs (Fig. 7) indicates that the differences are due to growth, although a greater number of large specimens are required to prove the trends conclusively. Increasing inflation is self-evident as the ventral margins of large specimens become more inflected and grossly thickened. The growth trends, the presence of indistinct costae on the shell surface of some large specimens, the more common occurrence of widely spaced costae on the inner surface of the outer shell layer (Pl. 6, fig. 1), the frequent occurrence of large specimens in concretions in the Cucullaea Assemblage Zone and small specimens in the matrix, and the linear trend shown by the number of chevron grooves on the cardinal area with increasing size (Fig. 8) indicates that the large and small specimens are conspecific. That species of Cucullaea are commonly extremely variable in shape and ornamentation, and show variation in proportions with growth has been described for the Jurassic C. contracta Phillips by Arkell (1929, p. 42-46), for Cretaceous species by Woods (1899, p. 49-64), and for the recent C. labiata (Solander) by Nicol (1950a). As the majority of large specimens are articulated and closed they cannot have been transported far. A possible reason for their large size is that they lived in a relatively more stable environment and were able to survive for a longer time than the populations represented by the small specimens in the concretions. A present-day example has been reported (Kristensen, 1957) for Ensis siliqua (Linnaeus) in Dutch coastal waters.

MATERIAL. 1255 specimens extracted from and remaining in concretions. Most specimens retain shell.

Occurrence. Cucullaea nebrascensis is common only in the Cucullaea Assemblage Zone, in both the Timber Lake Member and its westward extension into the Irish Creek lithofacies. It occurs in lesser numbers in some other assemblage zones, especially in the southern part of the Cymbophora-Tellinimera Assemblage Zone.

At Loc. 121, Grand River, one concretion (A1180) from the *Protocardia-Oxytoma* Assemblage Zone, Trail City Member, contained numerous small specimens, mostly single valves with many broken, and an articulated closed specimen occurred in the overlying banded beds below the base of the Timber Lake Member. An articulated closed specimen was also collected at Loc. 83, Bullhead lithofacies, Grand River, where it is associated with *Tancredia americana* and other species in the *Tancredia-Ophiomorpha* Biofacies.

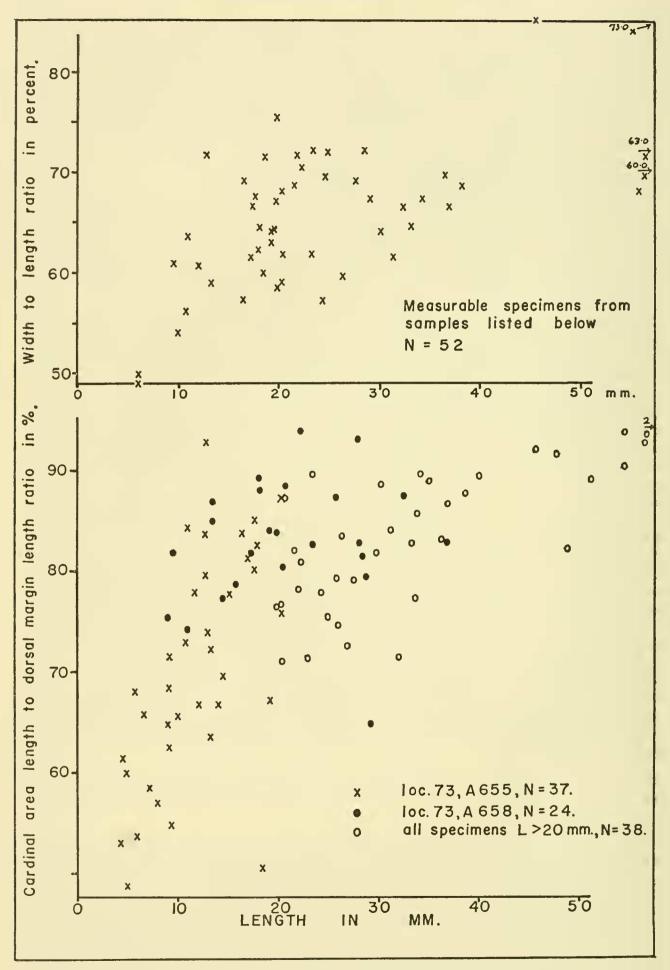


Fig. 7. Cucullaea nebrascensis. Scatter diagrams of length plotted against width to length ratio and cardinal area length to dorsal margin length ratio, both expressed as percentages, showing greater percentages with increasing size.

Comparisons. Three species of Cucullaea, nebrascensis, shumardi, and cordata, have been described from the general area of the type Fox Hills Formation; shumardi and cordata from "Moreau Trading Post, No. 5 of Series" by Meek and Hayden (1856a, p. 86), and nebrascensis from "between the Cheyenne and Moreau Rivers" by Owen (1852, p. 582). Meek (1876) redescribed and figured the three species which he differentiated on the basis of shape, shell thickness and shape of cardinal area. In all of these characters the "species" fall within the range of variation present in samples from concretions (fossil populations) made by Prof. K. M. Waage and the writer (Pls. 6, 7). As all other characters are common and no ecological differentiation is apparent, there can be no doubt that they are conspecific. The high form, represented by cordata, is much less common than the other shapes. Stanton's (1920, p. 22) specimen is specifically indeterminable.

A complex of species, most closely similar to C. capax Gabb (see Stephenson, 1941), has been described from the Gulf Coast and Atlantic Coastal Plains Upper Cretaceous sequences. The species have been differentiated qualitatively on the basis of shape, dentition, cardinal area, and ornamentation. It seems certain that quantitative studies would show only one or two species that have minor morphological differences related to habitat. Measurements made on a collection (YPM 9028, C. O. Dunbar, collector) of 33 left valves, 28 right valves and eight bivalved specimens of C. wadei Imlay (1937), the Cucullaea vulgaris of Morton (1830) and Wade (1926), and capax of Stephenson (1941), from Ripley Formation, Coon Creek, Tennessee show that the range of ratio percentages and means approximates closely those of the large specimens of nebrascensis, with mean values differing by less than 3 percent except for the ratio of dorsal margin length to length which is 10 percent smaller than for large nebrascensis but the same as for small nebrascensis. Wade (1926, p. 44) stated that the old (large) specimens of wadei show the greatest morphological variation with the ligament area becoming wider and the teeth "disappearing" with growth. He also noted that "older individuals" from Owl Creek and Coon Creek differ in length of hinge line and in the nature of the posterior extremity. When the complex of similar morphological factors

is considered these differences are probably phenotypic.

Cucullaea nebrascensis from the Western Interior is readily distinguished from wadei, and also probably from the capax "species" group, by the ornament, ligament number, umbonal characteristics and, to a lesser extent, the shape of the laminar teeth. Cucullaea nebrascensis has 50 to 90 costae on the largest specimens (height up to 19.3 mm) on which costae could be counted. Cucullaea wadei has about 190 to 210 (mean for four well-preserved specimens 199) at a height of 5 to 14 mm, resulting in a much finer pattern of costae which are crossed and attentuated laterally by fine growth lines giving a distinct punctate appearance to the shell. Cucullaea nebrascensis has a greater number of chevron grooves than wadei (Fig. 8), although there is considerable variation for large specimens and an overlap of fields where nebrascensis has exceptionally low numbers and wadei exceptionally high numbers. Note the one extreme case for each species. The sulcus on the posterodorsal flank varies considerably in prominence for both species. Strong sulci produce alate specimens. The degree of hooking of the central ends of the laminar teeth has also been used to distinguish species of Cucullaea. Whereas those of nebrascensis are rarely hooked but sometimes modified by prominent serrations, those of wadei are frequently strongly hooked with the hooks being massive and sometimes strongly curved. Cucullaea wadei specimens show a considerable variation in the degree and strength of hooking. The teeth of 30 of 70 specimens are essentially nonhooked. This indicates that the form of the teeth is of lesser taxonomic importance. Thus ornamentation and number of ligament grooves provide the best basis for the separation of the Western Interior species from wadei, and possibly from the capax species complex. Shape by itself is inadequate as most species apparently have the same range of variation. If the investigator is certain that he has adult and juvenile specimens then size may be of value.

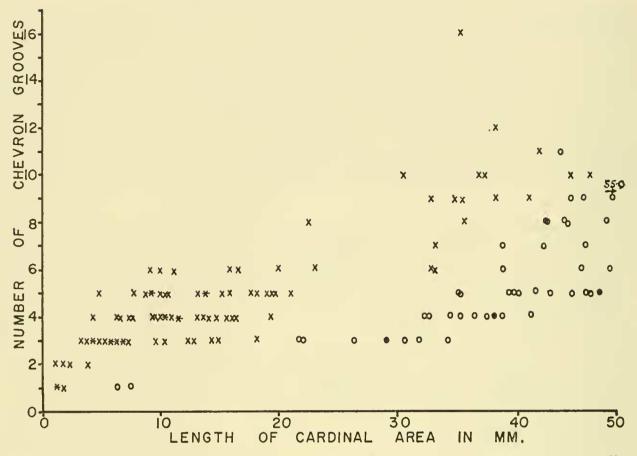


Fig. 8. Comparison of the number of chevron grooves on the cardinal areas of *Cucullaea* nebrascensis Owen and C. wadei Imlay. X = C. nebrascensis, Fox Hills Formation, N = 97 (* = >1 specimen).

X = C. nebrascensis, Fox Hills Formation, N = 97 (* = >1 specimen). O = C. wadei, Ripley Formation, Coon Creek, Tennessee, YPM 9028, N = 46 (• = >1 specimen).

PARALLELODON

AUTHOR. Meek & Worthen, 1866, p. 17.

Subgenus COSMETODON

Author. Branson, 1942, p. 248.

Type Species. By original designation (p. 248), Arca keyserlingii d'Orbigny (1850, p. 369), Oxfordian (Upper Jurassic), Russia and Europe.

Discussion. Branson (1942) clarified Arkell's (1930b) nomenclature and considered Grammatodon a genus with subgenera Parallelodon and Cosmetodon. Cox (1937, 1940) previously concluded that Grammatodon was generically distinct from Parallelodon, as did Kobayashi and Ichikawa (1950). The decision of the latter and Nicol's (1954) placement of Grammatodon in the Cucullaeidae require confirmation from a detailed review of the genus and related genera. The presence or absence of a byssal gape is difficult to prove for many fossil arcids, and some species of Grammatodon tend to be Cosmetodon-like in shape and dentition, whereas others possess a faint umbonal to ventral margin sulcus perhaps suggestive of a narrow byssal gape. Nevertheless, if Grammatodon is a distinctive genus, and this is accepted here, then the nomenclature will be as given by Driscoll (1961).

Previous workers (Meek, 1876, p. 81-83) included the species described below under Nemodon (Conrad, 1870), a genus characterized by laminar posterior and anterior teeth

that extend parallel to the dorsal margin for most of their length and are separated by a few rudimentary nodose teeth or a featureless interval. The hinge of the type species, N. conradi Johnson (1905), was poorly illustrated, but it is closely similar to that of N. eufaulensis (Gabb) (Gardner, 1916; Wade, 1926, Pl. 8, fig. 17; Stephenson, 1955, Pl. 15, figs. 8–12), and of other species, is distinctive, and the genus is undoubtedly valid as

suggested by Arkell (1930b, p. 309).

"Nemodon" sulcatinus (Evans & Shumard) is classed under Cosmetodon because it tends to narrow anteriorly, the greatest length is ventral, the posterior teeth are relatively more elongated than those of most species of Grammatodon, the umbones are situated anteriorly, are flattened and not prominent, the posterior carina is not very angular and, most important, a distinct umbonal to ventral margin sulcus is present on the left valve and at least on the umbone of the right valve. This sulcus results in a sinuous ventral margin and suggests the presence of a byssal sinus, which is also strongly indicated by a slight gape on larger specimens (see discussion below). These criteria are those used by Cox (1937) to differentiate Parallelodon from Grammatodon.

Parallelodon (Cosmetodon) sulcatinus (Evans & Shumard) (Plate 7, figs. 7–13; Plate 8, figs. 1–10)

Arca sulcatina Evans & Shumard, 1857, p. 39. Meek, 1864a, p. 9.

Nemodon sulcatinus (Evans & Shumard). Meek, 1876, p. 82-83, Pl. 15, figs. 6a,b.

[?]Nemodon canadensis Landes, 1940, p. 135, Pl. 1, figs. 1-3.

[?]Nemodon sulcatina (Evans & Shumard). Kellum, 1962, p. 58, Pl. 1, fig. 1; Pl. 3, fig. 16.

Description. Small, length of left valve 2.8 to 15.6 mm, inequivalve, with the right valve smaller than the left, inequilateral, moderately inflated. Shape variable, rectangular to rhomboidal, valves generally taper anteriorly with maximum height posterior to midlength. Some, especially the right valve, taper posteriorly. Maximum length below midheight, umbonal to posteroventral extremity angulation prominent. Height, width, anterior length and dorsal margin of left valve, respectively, 50 to 67.7 (N = 52, μ = 60.6%), 19.1 to 30.3 (N = 40, μ = 25%), 22.1 to 36.7 (N = 51, μ = 29.6%) and 76.6 to 93.8 (N = 44, μ = 85.7%) percent of length. Height, width, anterior length and dorsal margin of right valve, respectively, 48.2 to 66.7 (N = 50, μ = 59.4%), 17.4 to 29.2 (N = 37, $\mu = 22\%$), 26.2 to 35.5 (N = 37, $\mu = 30.5\%$) and 77.3 to 97.9 (N = 42, $\mu = 89.5\%$) percent of length. Length, height and width of right valve, respectively, 89.9 to 99.1 (N = 23, μ = 95.3%), 88.6 to 96.7 (N = 27, μ = 92.9%), and 81.8 to 92.9 (N = 19, μ = 87.9%) percent of left valve measurements, and combined width of valves 36.6 to 52.9 $(N = 16, \mu = 43.7\%)$ percent of length of the left valve. Dorsal margin straight, posterior margin straight or concave, anterior end rounded, ventral margin with a prominent sinuosity anterior to mid-length. Sinuosity corresponds with a sulcus of variable depth and width, markedly more distinct on left valve, often indefinite ventrally on right valve and rarely so on left valve. Umbones prosogyrous, flattened, widely separated. Cardinal area triangular with its apex anterior to umbones (Pl. 8, fig. 4), extends the length of dorsal margin, bounded by umbonal to dorsal extremity ridges, the posterior sharp and incurved, marked by fine striae parallel to commissure and with one to five ligament grooves posteriorly (Pl. 8, fig. 4). Anterior part of cardinal area slopes downward from commissure.

Multicostate; costae variable in number, spacing, pattern and strength, with primary, secondary and tertiary radial costae, the primary and secondary of equal size at ventral margin of medium- to large-size specimens. Costae rounded, wider than interspaces, normally most distinct and more widely spaced above a line between umbone and anteroventral extremity. Secondary costae intercalate at 0.7 to 1.4 mm, tertiary at about half the height of shell. Prodissoconch with fine growth lines. Valves with about equal numbers of primary and of total costae, 20 to 31 primary costae, with consistently one or two fewer on left valve, and 55 to 79 costae at ventral margin for specimens longer than

5 mm. Radial costae crossed by fine growth striae, and regularly by narrow growth depressions of variable strength which make costae nodose, nodules strongest and becoming spinose on anterior costae.

Hinge 77.4 to 94.3 (N = 25, μ = 85.4%) percent of dorsal margin, dorsal border straight, ventral border sinuous, gently concave ventrally, narrowest posterior to umbones. Prionodont, the teeth, particularly the central, extremely variable in number, strength and shape (Table 4 and Fig. 9). Anterior and posterior teeth radial on small specimens, becoming parallel to dorsal margin on large individuals, those at extremities sometimes directed ventrally. The posterior teeth extend parallel to dorsal margin for most of their length. Central teeth nodular, laminar, or coalesced nodular and straight, U-, L-, W-, or hook-shaped. The central space is sometimes smooth except for minute pits and nodules. Left valve with 4 to 8 anterior, 0 to 4 central, and 3 to 5 posterior teeth, the right valve with 4 to 6 anterior, 1 to 3 central and 3 to 6 posterior, the valves generally with one or two more anterior or posterior teeth respectively, but numbers may be equal or with one more posterior or anterior tooth respectively. Dorsal and

ventral surfaces and edge of teeth, and the matching sockets are finely serrated.

Adductor insertion areas impressed, subequal, the long axis of each inclined dorsally at a small angle to length axis of shell. Anterior insertion slightly smaller, subquadrangular, with a fine extension from posterodorsal extremity, sometimes deeply impressed, bounded ventrally and sometimes dorsally by a fine ridge. Posterior insertion subrectangular, tapers slightly anteriorly, a fine anterodorsal extension from center of anterior margin rarely present, bounded ventrally by a strong ridge and posteriorly by a weak ridge, both of which extend into the umbonal cavity. Pedal insertion areas weakly impressed, under ventral margin of hinge; the posterior narrow, rectangular, extending from above anterior end of posterior adductor to the anterior end of the ventral posterior lamellar tooth, the anterior above the anterior adductor, an irregular swelling of a pallial impression that extends from anterodorsal end of adductor along ventral margin of hinge to near posterior pedal insertion, where it reflexes and passes anterodorsally into umbonal cavity and toward anterior adductor for a short distance. A small, often strongly impressed linear insertion area, the pedal elevator of authors, is situated in the umbonal cavity ventral to the anterior end of posterior pedal insertion. Up to three small muscle insertion pits are sometimes present anterodorsally to the linear insertion area. A narrow ridge, often steep-sided, corresponding to the external sulcus, extends from umbo to ventral margin of left valve but is weak or absent on right valve. Ventral margin of right valve serrated on both sides of sulcus; the posterior serrations tend to be spinose. Serrations interlock with short, strong crenules and grooves situated between smooth pallial band and smooth margin of left valve; the crenules are sometimes bifid. The interval across the sulcus of the left valve is smooth or with a fine growth ridge (Pl. 8, fig. 8).

Maximum thickness of ostracum of large specimens is 0.7 mm, composed of three layers. An outer concentric cross-lamellar layer, a middle very thin myostracum and a

inner concentric cross-lamellar layer.

Types. Whereabouts of the holotype of Arca sulcatina is unknown. Type locality: "Wood's Fork, 3 miles from Grand River", South Dakota. Stratigraphic position: Fox Hills Formation, probably from Limopsis-Pseudoptera Assemblage Zone. Holotype of Nemodon canadensis Landes, GSC Cat. No. 9345, by original designation. Type locality: Manyberries Creek, Southern Alberta, Canada. Stratigraphic position: Arctica ovata horizon, Bearpaw Formation.

Types held at YPM are: hypotypes YPM 23911-43, 24020-27.

Discussion. A thin band of outer ligament material (Owen, 1959, p. 218, fig. 4) is preserved in the ligament grooves of most articulated specimens and some single valves on which the cardinal area was exposed. Inner ligament material occurs between the grooves on certain specimens, suggesting that it was also present but was mostly removed during preparation of the area. The species probably possessed an amphidetic duplivincular type of ligament (Newell, 1942), yet the restriction of ligament grooves to the

posterior portion of the ligament area is noteworthy. The first, and strongest, groove appears a short distance from the prodissoconch and produces a marked step in the length profile of the cardinal area. The second groove enters at varying distances, 0.7 to 2.2 mm, and the succeeding ones very rapidly thereafter. The lack of anterior grooves may be due to noninsertion of the outer (laminar) ligament into sockets, or to the suppression of the anterior outer layer bands until a certain size is reached. The controlling factor may be the relative shortness of the anterior part of the ligament area. Of interest in this respect is Newell's (1937, p. 29) observation that for the extant Arca transversa Say the first formed groove is entirely posterior. That this is widespread amongst arcid genera was indicated by an examination of recent species held in the collections of Peabody Museum, Yale University. For example, two to seven posterior grooves appeared before the first anterior one on specimens from a suite of Arca umbonata Lamarck. The variation of ornamentation and dentition of sulcatinus is marked. The ornament varies mostly in the numbers and strength of costae on each valve and in the distribution of tertiary costae. Tertiary costae are most common anteriorly, posteriorly and on the main disc of the shell below mid-height. The costation pattern is modified by the form of the sulcus. A deep broad sulcus suppresses tertiaries posterior to sulcus and results in primary and secondary costae of equal magnitude. A narrow deep sulcus modifies the pattern only in its immediate vicinity, and an indefinite sulcus has little effect. A discrepancy in the number of costae on each valve is most evident anterior to the sulcus, with the left valve generally having fewer and stronger primaries (Pl. 7, figs. 7, 8). This is usually counterbalanced posteriorly so that the two valves have about equal numbers of costae along the ventral margin.

The teeth were arbitrarily divided into three groups: Anterior and posterior segments, with laminar teeth arranged radially to the center of the hinge or parallel to the dorsal margin, with an intermediate zone of central teeth of diverse form (Fig. 9). Fusion of central teeth to adjacent posterior and/or anterior laminar teeth complicates the separation. In these cases the complex was counted as two teeth. The long laminar posterior teeth fluctuate in width and many show slight gaps probably due to growth rather than to fusion of segments. The short ventral posterior and anterior laminar teeth often continue toward the center as the border of a socket and/or the ventral margin of the hinge. Many teeth at the central end of the anterior and posterior segments flexure to parallel the dorsal margin and rapidly taper to an end. The diversity of the central teeth is emphasized by the fact that the form and pattern is not duplicated on 19 left or 15 right valve hinges.

Small specimens less than 5 mm long appear to have perfect closure in the region of the sulcus (Pl. 7, fig. 10). Several large specimens show a distinct wedge of matrix between the two valves. This does not seem to be due to compaction distortion or fracturing. The presence of a byssal gape is supported by the tendency for matrix to adhere in the sulcus region and the absence of crenules across the sulcus margin of the left valve.

MATERIAL. About 2000 specimens extracted from and remaining in concretions. Most are steinkerns as the shell, because of the inequivalveness and growth depression-costation pattern of ornamentation, readily breaks away.

Occurrence. The species is common only in the *Limopsis-Pseudoptera* Assemblage Zone where it is associated with *Limopsis* in particular and sometimes becomes a codominant giving *Limopsis-Parallelodon* assemblages. One or two valves were collected from concretions at localities in other units.

Comparisons. The specimens on which Evans and Shumard (1857) based the original description were steinkerns collected from the vicinity of Grand River. Those described by Meek (1876) came from the "Yellowstone, 150 miles above its mouth" and also lacked well-preserved shell. The above description represents a complete revision. Not observed by the above workers are the variation in dentition, shape and ornament, the

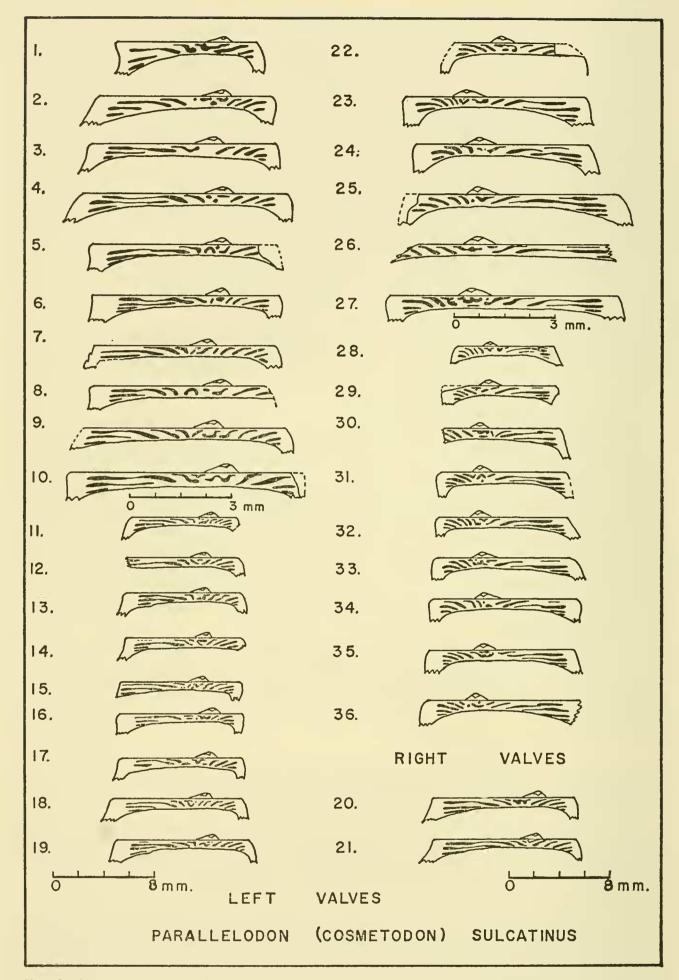


Fig. 9. Arrangement and shape (schematic) of teeth on hinges of *Parallelodon (Cosmetodon)* sulcatinus (Evans & Shumard). Note variation of teeth on the central segment.

TABLE 3. Identification of teeth in Figure 9.

								_
1.	YPM 23911	Loc. 243	A1070	19.	YPM 23942	Loc. 238	A1043	
2.	23916	199	677‡	20.	23943	243	1013	
3.	23922	191	561	21.	23918	191	561	
4.	23915	199	677‡	22.	23926	105	1107	
5.	23921	191	561	23.	23916	199	677	
6.	23925	105	1107	24.	23923	191	561	
7.	23917	200	680	25.	23915	199	677	
8.	*	191	561	26.	23936	235	1020	
9.	23914	199	677	27.	23924	199	561	
10.	23931	231	991	28.	23920	222	618	
11.	23913	199	677	29.	23932	222	618	
12.	23935	235	1020	30.	23937	235	1020	
13.	23940	242	1061	31.	23939	237	1038	
14.	23930	231	991	32.	23912	199	677	
15.	23919	191	561	33.	23938	103	983	
16.	23934	235	1021	34.	23933	95	933†	
17.	23941	242	1061	35.	23929	231	991	
18.	23928	234	1014	36.	23927	234	1014	

^{*} Destroyed after drawn

inequivalveness and the lack of marginal crenules on the right valve. Evans and Shumard also remarked, contrary to fact, that the sulcus was stronger on the right valve.

Parallelodon sulcatinus is distinctive and cannot be confused with any other species of the type Fox Hills fauna. Although discordance of valve features is not uncommon in the Arcacea (Nicol, 1958), the degree of inequivalveness of sulcatinus is exceptional. In general shape, ornament and occurrence of a weaker sulcus on the right valve, the specimens of Nemodon eufaulensis (Gabb), from Crowley Ridge, southeastern Missouri, figured by Stephenson (1955) are similar to sulcatinus. Specimens lacking or with a weak sulcus resemble canadensis Landes which here is considered conspecific.

PTERIACEA

TENUIPTERIA

Author. Stephenson, 1955, p. 110.

Type Species. By original designation of Stephenson (1955, p. 110), Inoceramus argenteus Conrad (1858, p. 329), Owl Creek Formation, Maestrichtian, Gulf Coast, North America.

Discussion. For a full discussion of the characteristics of the genus and species included in the genus, see Speden (in press), who confirmed Jeletzky's (1962, p. 1014; Jeletzky and Clemens, 1965) skepticism of the generic placing of *Inoceramus fibrosus*.

The YPM collections contain Upper Cretaceous specimens of "Inoceramus" resembling barabini Morton. These are suboval, strongly inflated with prominent umbones, thin shelled with an outer prismatic and a thicker inner nacreous layer, and have a small anterior ear and a ligament area resembling that of Tenuipteria. The narrow ligament area proved to be L-shaped with a marked step (YPM 24055; Pl. 10, fig. 3), or more or less flat (YPM 24452), and with the dorsal one third or half having a series of small shallow ligament pits which become smaller and less definite toward the umbones. The muscle insertion pattern of two specimens (YPM 24053, 24054) labeled Endocostea

[‡] Center of hinge later damaged

[†] Reconstruction from matching right valves

typica White, from Converse County, Wyoming, Pierre Shale resembles that of Tenuipteria with the insertions situated close to the margin of the inner shell layer and the posterior adductor situated posteroventrally and overlapping an endocosta if developed. However, the pallial line consists of a series of discrete pits, and a line of smaller discrete pits extends dorsally from the anterior of the two anterodorsal byssal-pedal insertions across the umbone, along the dorsal margin and down to the posterior adductor. A large specimen from the "Pierre", Converse County, Wyoming (YPM 24052) has a band of small discrete insertions in groups of two or three which appear to correlate with a larger insertion in the pallial line directly above. Most of the above specimens have the hollow endocosta characteristic of Whitfield's (1877, 1880) genus Endocostea (considered a subgenus by Anderson, 1958, p. 105). This endocosta is not always developed, as mentioned by Meek (1876, p. 50), and Toots (1964) considers it to be due to a parasite. As the musculation pattern is different from that of both Inoceramus and Tenuipteria and as the form of the ligament is intermediate between these two genera, Endocostea is probably a valid genus. Its pterioid-like musculation and the presence of numerous small ligament pits suggest a close relationship to Inoceramus. The relations of Endocostea and the systematics of a complex of inoceramiid-like species resembling barabini require study.

Tenuipteria fibrosa (Meek & Hayden) (Plate 8, figs. 11–18; Plate 9, figs. 1–16)

Avicula? fibrosa Meek & Hayden, 1856a, p. 86-87.

Pholadomya fibrosa (Meek & Hayden). Meek & Hayden, 1856c, p. 283.

Pinna fibrosa (Meek & Hayden). Meek, 1864a, p. 9.

Avicula (Pseudoptera) fibrosa (Meek & Hayden). Meek, 1873, p. 489.

Pteria (Pseudoptera) fibrosa (Meek & Hayden). Meek, 1876, p. 36-37, Pl. 17, figs. 17a-d. Whitfield, 1880, p. 386, Pl. 7, fig. 5. Whiteaves, 1885, p. 32, Pl. 4, fig. 1.

Inoceramus (Actinoceramus) whitii Toepelman, 1922, p. 63.

Inoceramus (Actinoceramus) fibrosus (Meek & Hayden). Dobbin & Reeside, 1929, p. 20.

Tardinacara (Pseudoptera) fibrosa (Meek & Hayden). Elias, 1931, opp. p. 58, p. 124, 130. Searight, 1934, p. 4.

Inoceramus (Actinoceramus) fibrosa (Meek & Hayden). Russell, 1940, p. 88.

Inoceramus fibrosus (Meek & Hayden). Landes, 1940, p. 136–137. Cobban & Reeside, 1952, p. 1020, and correlation chart. Jeletzky, 1962, p. 1011–1014, Pl. 141, figs. 4–7. Seitz, 1959, p. 123–124 (? synonymous with I. tegulatus Hagenow (1842, p. 559)).

Inoceramus radiatus Kellum, 1962, p. 57, Pl. 5, fig. 17 (non Heine, 1929, p. 105, Pl. 18, figs. 68, 69).

Inoceramus cobbani Kellum, 1964, p. 1006 (new name for I. radiatus Kellum).

Inoceramus? tegulatus Hagenow, 1842 (non Ødum, 1922). Jeletzky, in Jeletzky and Clemens, 1965, p. 957.

Tenuipteria fibrosa (Meek & Hayden). Speden (in press), Pl. 1, figs. 1-6.

Description. Length 5 to 55 mm, equivalve, inequilateral, slightly to moderately inflated, maximum inflation about mid-height and along anterior margin. Umbones near anterior end of dorsal margin, prosogyrous, not prominent, and project only slightly above the dorsal margin. Shape extremely variable, submytiloid to subquadrangular. Height, anterior length and width are, respectively, approximately 85 to 100, 8 to 15 and 12 to 27 percent of the length for the outline of the inner shell layer, and the prosoclinal growth axis forms an angle of 40 to 50 degrees with the straight or slightly arched dorsal margin. Posterodorsal margin rounded, lacking a posterior ear. Anterior ear distinct, always present, relatively small but of variable size, the internal surface sloping inward on left valve, sometimes strongly, that on matching right valve approximately vertical or sloping outward, external surface of ear with one or two faint furrows, and delimited by a narrow groove from the moderately to strongly inflexed anterodorsal margin. Demarcation groove strong and ending in a byssal notch if margin strongly inflexed, or weak and without external evidence of a notch if inflexion is slight. Anterodorsal margin

with a byssal gape of variable width. Ventral margin of ear and margin of area below ear sometimes reflexed outward to form a flange of variable prominence (Pl. 9, fig. 13). Ornamentation extremely variable, with fine growth lamellae and round-topped concentric plications of variable strength, ventral limb the steeper, narrower than the interspaces, normally crossed by faint, narrow, shallow radial sulci which divide the concentric plicae into subquadrangular flat-topped nodes. Radial sulci sometimes very strong and deep, especially on anteroventral part of shell on either side of axis of maximum inflation, are absent from posterodorsal flank of valve, appear at 5 to 20 mm, and are apparently absent rarely on specimens longer than 20 mm.

Ligament area extends length of dorsal margin, inclined at 50 to 60 degrees to the horizontal, generally strongly concave and almost semicircular in cross-section and so like an open tube, sometimes L-shaped with a wider, slightly concave dorsal limb and a flat ventral limb inclined at 10 to 30 degrees to the horizontal, marked by fine longitudinal striae separated by much wider depressions, striae often faint and sometimes absent on ventral part of ligament, area usually overhung by dorsal margin in vicinity of umbones. Posterior insertion area large, elliptical to pear-shaped, tapering posterodorsally where deeply impressed at extremity, anterior margin with an indentation of variable prominence, situated at posteroventral extremity of inner shell layer close to its junction with outer shell layer; rarely preserved. Two small anterodorsal insertion areas (pedalbyssal retractors) sited in the umbonal cavity: a small oval insertion, one tenth the size of the posterior adductor, anterior to the line of maximum inflation, and a slightly larger subrectangular scar posterior to the line of maximum inflation (Pl. 9, fig. 9). Pallial line on inner shell layer close to junction with outer shell layer, a narrow continuous band with irregularly spaced swellings from posterior adductor to above midheight of shell, then continues as a series of four to eight small discrete oval or linear scars. Three to five small oval impressions may occur close to the dorsal margin above the two insertions in the umbonal cavity.

Ostracum very thin and fragile, maximum observed thickness 0.7 mm, rarely exceeds 0.5 mm, composed of a thick outer prismatic layer, the prisms aligned perpendicular to the outer surface, and a thin, inner pearly nacreous layer one quarter to one sixth the thickness of the outer layer. The outer layer extends considerably beyond the inner as a broad flange and comprises exclusively the anterior ear and the ligament area which is two to three times thicker than the main disc of the valve (Pl. 8, fig. 17). Part of the anterior ear is sometimes composed of homogeneous calcite. The internal surface of the umbonal cavity is marked by fine irregular striae which approximately parallel the growth axis. Small plaits obliquely cross the internal surface of the shell on the anterior area. Many specimens have a faint ridge along a line extending from the dorsal margin posterior to the umbone to the anterodorsal end of the posterior adductor.

Types. Lectotype of Avicula? fibrosa, by subsequent designation of Meek (1876, Pl. 17, fig. 17a), USNM 460, a steinkern of a right valve, oblique length 34.7 mm. Type locality: Forks of Cheyenne River, South Dakota. Stratigraphic position: Pierre Shale, Upper Cretaceous, Maestrichtian.

Types held at YPM are: hypotypes YPM 24028-39, 24643-48, and 24742.

Discussion. Because of the fragility of the shell complete specimens are very rare. The presence of the posterior adductor scar is sometimes the only proof that a specimen is complete. The margin of the outer shell layer may or may not conform to the outline of the inner shell and, as the dorsal margin of the ligament does not parallel the dorsal outline of the inner shell layer but diverges from it by angles of 10 to 25 degrees (Pl. 8, fig. 14), measurements bear little resemblance to the true form of specimens. The variability of most morphological features is marked. It is the association of gross form, possession of a distinct anterior ear, and the presence of concentric plicae and radial sulci, the latter being faint and not evident on poorly preserved steinkerns, and absent on small specimens, that are characteristic of the species. Jeletzky (1962) has discussed the variability of the ornamentation. Smooth, or faintly or strongly radially sulcate specimens

may occur in one sample. Those with weak to moderately strong radial sulci dominate samples from concretions in Fox Hills Formation. Specimens with strong radial sulci, closely resembling the type specimen (Meek, 1876, Pl. 17, fig. 7a), are present in collections from the Mobridge Member of Pierre Shale (A336), Trail City Member (A232, A270), and Timber Lake Member (A340).

Comparison to mytiloid genera (see Newell, 1942, p. 30, fig. 6) indicates that the posterior adductor insertion includes the posterior pedal insertion and that a pallial attachment or gill suspensory attachment may coincide with the ridge extending from the dorsal end of the posterior adductor toward the umbones. Many specimens retain pearly fibrous inner ligament material. The ligament was probably parivincular. The minute transverse striae considered by Meek (1876, p. 37) to occur on the ligament are due to weathering of the underlying prismatic shell structure.

MATERIAL. About 1300 mostly incomplete specimens as individuals and in selected blocks and concretions.

Occurrence. Although it occurs in all major assemblage zones the species is common only in Lower nicolleti Assemblage Zone (80.8%), where it occurs as a codominant in assemblages with Discoscaphites and sometimes Protocardia, and as scattered specimens. Some 8 percent were collected from the Timber Lake Member, with most specimens coming from the undifferentiated sequence south of the Moreau River. Except in Lower nicolleti Assemblage Zone, Tenuipteria fibrosa mainly occurs as scattered specimens in concretions. It normally occurs as codominant with Discoscaphites in the Upper nicolleti Assemblage Zone, occasionally in the Protocardia-Oxytoma Assemblage Zone, and at Loc. 32 (Mobridge Member, Pierre Shale).

The low ratio of articulated to disarticulated specimens of 0.1:1 to 4:1 in all (= 16) samples of more than 20 specimens and their incompleteness are reflections of the fragility of the shell and relative weakness of articulation. The general lack of abrasion, the nondispersion of fragmented specimens, the rather consistent ratio of left to right valves of 0.1:1 to 1.65:1 for the same samples, and the admixture of larger and smaller species are indicative of rather little transportation. Because of the presence in most samples of a significant number of valves unable to be classified as left or right, the above figures are rather uncertain. Yet the relative consistency of the ratios suggests that the unclassified valves are probably present in approximately equal proportions.

In the Western Interior T. fibrosa ranges from the Baculites baculus zone through the Timber Lake Member of the Fox Hills Formation (Cobban and Reeside, 1952). It is commonly reported from the Pierre Shale (Robinson and others, 1959). Jeletzky (1962, p. 1012) states that it is known only from the upper part of the Bearpaw Formation in south-central Canada.

Comparisons. Well-preserved specimens of this distinctive species cannot be confused with any other Western Interior Upper Cretaceous species. The right valve of *Tenuipteria argentea* (Conrad; Stephenson, 1955) and some "Inoceramus" species have similar ornament, and fragments could be misidentified. Whitfield's (1880, Pl. 7, fig. 5; USNM 12332) specimen is generically and specifically indeterminable. The specimen from Belly River, Northwest Territories described by Whiteaves (1885, p. 30, Pl. 4, fig. 1), although perhaps indeterminable, cannot be distinguished from specimens of fibrosa. Nor can the specimen figured by Kellum (1962) which resembles juveniles present in collections from the type area of the Fox Hills Formation. Toepleman's (1922) description of his I. (Actinoceramus) whitii leaves little doubt that it is conspecific with fibrosa. As noted by Jeletzky (in Jeletzky and Clemens, 1965, p. 958), whitii is one extreme variant of an extremely variable epifaunal species.

Jeletzky (1962, p. 1012) placed the externally similar *Inoceramus caucasicus* Dobrov (1951; and Dobrov and Pavlova, 1959), Caucasus and Russian platform, Upper Campanian through lower Maestrichtian, in synonymy under *fibrosus*. Later Jeletzky (in Jeletzky and Clemens, 1965) placed *fibrosus* and *caucasicus* as synonyms of *I*.?

tegulatus Hagenow non Ødum (1922) and separated Ødum's specimens as a distinct species, which he named dobrovi Jeletzky. Seitz (in Jeletzky and Clemens, 1965, p. 955) and Jeletzky's recognition of an equivalve "Avicula-like" form with insignificant umbones (tegulatus) and an inequivalve subquadrate form with a prominent projecting umbone on the left valve and a flattish right valve (dobrovi) is a marked step forward in our

understanding of the Maestrichtian tegulatus-like inoceramiids.

In my review of the species included in the genus Tenuipteria I concluded that the information presently available necessitates treating the European tegulata and the North American fibrosa as distinct species, although caucasica may be conspecific with tegulata (Speden, in press). Jeletzky (1962) considered fibrosa and tegulata to have identical stratigraphic ranges, Upper Campanian and Lower Maestrichtian, though many workers (Cobban and Reeside, 1952; Seitz, 1959) restrict fibrosa to the Maestrichtian in the Western Interior. Even if tegulata is conspecific with fibrosa, there are no reasons why their local range zones (teilzones) should be the same in the different continents, and conceivably fibrosa could range through the Maestrichtian in the Western Interior.

PSEUDOPTERA

AUTHOR. Meek, 1873, p. 489.

Type Species. By original designation, Avicula anomala Sowerby (1836, p. 342), as illustrated by d'Orbigny (1843-47, p. 478, Pl. 392), lower Turonian, Europe.

Discussion. Meek (1873) proposed the taxon, as a subgenus of Avicula (= Pteria), while describing A. (Pseudoptera) propleura from the Frontier Formation (Cenomanian-Turonian), Coalville, Utah. The subgenus was distinguished by its "subtrapeziform" shape and lack of well-defined anterior and posterior ears and of a byssal notch. Meek had no knowledge of the hinge and musculation of the type species or of other species he included in the subgenus. Woods (1905, p. 65) considered that the species figured by d'Orbigny, collected from the lower Turonian at Le Mans, France, belonged to a different species. The morphological features used by Woods might not be of sufficient rank to warrant separation. Woods (1905, p. 435), on the basis of illustrations of hinges of species included in Pseudoptera, transferred the subgenus to Gervillia. Stephenson (1952, p. 70) gave Pseudoptera generic status.

Pseudoptera, as represented by the species described by Stephenson (1952, 1956), is differentiated from Gervillia by its strong inequivalveness, by the presence of radial costae which may be strong (P. serrata Stephenson), faint, or present only on juvenile specimens (P. subtortuosa), by the lack of a byssal notch, and by the presence of only one linear tooth under the anterior ligament pit and an indefinite (subtortuosa) or strong (P. vivana Stephenson) lamellar lateral tooth. Gervillia is generally considered (Arkell, 1933; Hayami, 1957) to be equivalve or inequivalve, to lack radial ornament, to have a strong byssal notch, and to have two or more linear teeth along the anteroventral

margin of the ligament.

Stanton (1893, p. 75) states that propleura has two or three anterior linear teeth, which suggests a relationship to Gervillia, yet the presence of anterior radial costae, absence of a byssal notch, and the strong inequivalveness are indicative of Pseudoptera. Meek's (1876, Pl. 16, fig. 7c (idealized); USNM 356) specimen has, in addition to the strong anterior tooth, faint protuberances simulating other teeth on an abnormally wide shelf below the anterior three ligament pits. The number of teeth may be of minor taxonomic significance in Gervillia and morphologically similar genera. For example, G. aviculoides (Sowerby; Arkell, 1933, p. 203), Middle Jurassic, Great Britain, has traces of two obscure rudimentary teeth, and G. (Odontoperna) bouei (Hauer; Frech, 1902, p. 617), Upper Triassic, has one or two teeth and the anterior part of its hinge is similar to that of P. subtortuosa.

When considered together the four features enumerated above are considered of generic rank, and *Pseudoptera* is here treated as a genus. The systematic position of the type species *anomala* and certain other species included in *Pseudoptera* requires a knowledge of their hinges.

Pseudoptera subtortuosa (Meek & Hayden) (Plate 10, figs. 4–11; Plate 11, figs. 1–9; Plate 12, figs. 1–2)

Gervillia subtortuosa Meek & Hayden, 1856c, p. 276. Meek, 1876, p. 65–66, Pl. 16, figs. 7a-c. Gervillia recta Meek & Hayden, 1861, p. 441. Meek, 1876, p. 66–67, Pl. 29, figs. 1a,b. [?] Gervillia recta var. borealis Whiteaves, 1885, p. 35–36, Pl. 4, figs. 2; 2a,b. [?] Gervillia stantoni McLearn, 1920, p. 55, fig. 1.

Description. Adult specimens large, length of left valve of specimens 5.1 to greater than 135 mm, strongly inequivalve and inequilateral, inflation slight. Shape variable, gervillioid, strongly prosoclinal, weakly to strongly twisted for medium to large specimens, especially along the anterodorsal margin. Anterior margin broadly convex, posterior weakly concave to straight, posteroventral part of shell rectangular or tapering with the margin broadly or narrowly convex. Left valve two or three times more inflated than the right, maximum inflation of both valves along the ridge extending from the umbone to the posteroventral margin, narrowest and greatest on dorsal third, flattening ventrally especially on right valve which becomes almost flat. Inflated area triangular, widening from umbones, bordered dorsally by an umbonal to posterodorsal angulation and sulcus above which the shell becomes alate. Posterior ear with a pointed or rounded attenuation on some small and rare large specimens. Umbones near anterior extremity, about one twelfth to one sixteenth of length of ligament area from anterior end, only that of left valve projects slightly above dorsal margin. Presence or absence of a byssal notch uncertain, possibly present just beneath anterior ear. Height, oblique length, length of dorsal margin and inflation, respectively, 56.3 to 107.3 (N = 43, μ = 81.5%), 107.7 to 132.9 (N = 43, μ = 116.9%), 40.4 to 86.3 (N = 42, μ = 59.5%) and 5.6 to 16.5 (N = 41, μ = 11.8%) percent of length of left valve. Length of specimens of right valve 3.9 to 122.7 mm, with height, oblique length, length of dorsal margin and inflation, respectively, 61.0 to 97.9 (N = 66, $\mu = 78.3\%$), 103.1 to 140.6 (N = 66, $\mu = 117.3\%$), 51.2 to 94.8 (N = 64, $\mu = 67.6$) and 3.1 to 10.3 (N = 49, μ = 5.9%) percent of length. Right valve smaller and fits inside left valve, central portion of anterior margin sometimes reflexed outward to accommodate to the twisting of valves. Length, height, oblique length and inflation of right valve, respectively, 73.6 to 96.8 (N = 25, μ = 88.3%), 73.3 to 93.0 (N = 25, μ = 83.7%), 78.9 to 94.0 (N = 25, μ = 88.1%) and 24.4 to 75.0 (N = 25, μ = 44.1%) percent of the left valve measurements.

Outer surfaces of inner and outer shell layers ornamented with fine growth striae and lamellae, and sometimes by fine faint radial costae which are more common on the inner layer and rare on the outer, and most conspicuous and sometimes present only along the umbone to posteroventral margin ridge. Costae become less distinctive with growth.

Ligament area extends the length of dorsal margin, narrows toward extremities, widest adjacent to umbones where 0.6 to 1.2 mm wide in specimens greater than 50 mm long, inclined at about 30 to 40 degrees to the vertical anteriorly, changing to 10 to 20 degrees posteriorly. Multivincular; ligament pits deep, narrower than interspaces, with undercut sides, more closely spaced with increasing size, three to four pits on specimens less than 25 mm long, and up to nine on large specimens. The anterior one or two pits under the umbone triangular with the apex not reaching the ventral margin of ligament area. Interspaces and pits marked by fine striae that parallel the ventral margin. On the left valve the surface of the ligament area anterior to the last pit has a posterodorsally directed, low rounded ridge bordered on both sides by faint, shallow furrows. These are matched on the right valve by weak ridges and a central more distinct furrow. Beneath the anterior pit the ventral margin of the ligament area is shelflike with a postero-

ventrally directed weak to strong linear anterior tooth, a continuation of the ridge across the ligament, a furrow situated under the ligament pit, and behind this sometimes a weak protuberance suggestive of a second tooth. A conical cavity extends dorsally under the ligament anterior to the linear tooth (Pl. 11, fig. 2). Right valve has a matching massive edentulous shelf below the anterior ligament pit. On many large specimens a linear lateral tooth of variable length and strength may be present on each valve immediately under the ligament area and above the posterior adductor insertion area.

Monomyarian; posterior adductor insertion area large, moderately impressed, irregularly elliptical, long axis vertical, length equal to about one quarter of height of shell, situated in upper half of height posterior to mid-length, marked by growth lines. An oval to subquadrangular, moderately impressed insertion area is situated close to anteroventral extremity of the adductor. A small deeply impressed oval insertion lies at the posteroventral margin of the umbonal cavity, and an oval to linear insertion area occurs at the base of the conical cavity of the left valve and the matching weak cavity of the right valve (Pl. 10, figs. 8, 9). A variable number, one to three, of oval or coalesced linear insertions occurs in the umbonal cavity of the right valve and rarely on the left valve. The pallial line, a linear pattern of 11 to 16 discrete oval or coalesced-linear weakly impressed scars, extends in a slight curve from the small scar at the anteroventral margin of the adductor along the umbonal ridge to the umbone. In some cases the pallial line is on the anterior flank of the umbonal ridge, especially on the left valve.

Ostracum up to 4.5 mm thick in the umbonal region and 3.0 mm elsewhere for large specimens, of two layers. A thin outer prismatic layer and an inner pearly lamellar nacreous layer four to five times thicker than outer layer. Outer layer extends as a border around all but the dorsal margin of the shell, widest ventrally where it may be 1 to 4 mm wide on specimens up to 50 mm long. Border may be elongated antero- or posteroventrally and is narrow or absent on right valve. Internal surface of inner layer smooth or sometimes with weak radial costae, especially on the posterodorsal flank.

Types. Lectotype of Gervillia subtortuosa, USNM 356, by subsequent designation of Meek (1876, in caption to Pl. 16, fig. 7a), an abnormally twisted specimen. Type locality: 300 miles above Fort Union on the Missouri River. Stratigraphic position: Pierre Shale, Upper Cretaceous (Campanian-Maestrichtian). Lectotype of Gervillia recta, USNM 7843, by subsequent designation of Meek (1876, in caption to Pl. 29, fig. 1a), a two-valved steinkern with some shell, L = 34.5, H = 16.5, OL = 36.5, ½ W = 3.2 for left valve and 1.0 mm for right valve. Type locality: Deer Creek, near North Platte, Wyoming. Stratigraphic position: Fox Hills Formation, ?Maestrichtian. Holotype of Gervillia stantoni, GSC Cat. No. 5669, by original designation (McLearn, 1920, p. 55). Type locality: Smoky River, Alberta. Stratigraphic position: Bad Heart Sandstone Member, Smoky River Formation, Santonian (Stott, 1963).

Types held at YPM are: hypotypes YPM 24040, 24042, 24043A, 24043B, 24045-51, 24487, 24744.

Discussion. The measurements were made as shown on Figure 10. Because of the twisting of the shell, which makes measurement of inflation very difficult, and the variable extension of the outer shell layer beyond inner, the measurements give only an order of magnitude. This is compounded by the necessity of making most measurements on the outline of the inner layer, for the outer layer rarely leaves an impression. Also, the mode of occurrence of the species as closely packed randomly oriented or aligned masses makes extraction difficult, and the ears are generally incomplete. The outline of the margin of the outer shell layer usually corresponds with the form of the inner layer, and the proportions are approximately the same although of different magnitude. Frequently the antero- or posteroventral extremities are clongated, and the outline of the margin of the outer shell diverges markedly from that of the inner shell layer. This causes the wide variation in measurements given above. Many recent pterioid (Pteria, Pinctada) and isognomonid (Isognomon) genera also have a margin of outer prismatic shell layer of variable width and shape.

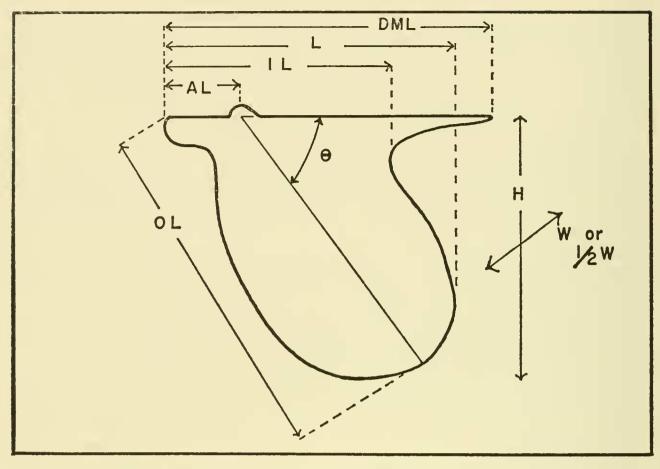


Fig. 10. Orientation of measurements made on pterioid-shaped species.

L = Length

W = width

OL = oblique length

IL = length from anterior extremity to base

of posterior ear

DML = length of dorsal margin

H = height

1/2 = width of one valve

AL = anterior length

 Θ = angle measuring prosoclinality

The pattern of muscle insertion areas is closely analogous to that of pterioid genera such as Pinctada (see Newell, 1937, fig. 1). The basic units, the posterior adductor, the pallial line of small discrete insertions, the presence of two strong pedal elevator insertions in the umbonal region, and one pedal retractor insertion closely associated with the adductor are similar. Minor differences are the variability in number and pattern of accessory insertions in the umbonal area and the occasional insertion pits on either side of the impressed posterior pedal elevator insertion area. The major difference is in the size and position of the pedal retractor insertion area. Most modern pterioid and isognomonid genera have a curved or V-shaped adductor with a relatively large pedal insertion fused or discrete from it on the anterior side at about mid-height of the insertion area or between the arms of the adductor. Examination of specimens of the recent Isognomon isognomon (Linnaeus) in the YPM collections shows that although the position is constant the degree of fusion of the pedal insertion is variable. For most pterioid genera it is fused to the adductor. The pedal retractor insertion area of Pseudoptera subtortuosa is relatively small, discrete, and situated at the anteroventral extremity of the adductor. The phylogenetic significance of this is at present unknown, but it would be possibly a simple step for the adductor to reflex and for the pedal insertion to migrate to a central position. A strong horizontal cross-ridging is present on the anterior part of some adductor insertion areas and probably represents an interaction of the catch part of the muscle with the shell. As none of the well-preserved Fox Hills specimens possesses an anterior insertion like that on the specimen figured by Whiteaves (1885, Pl. 4, fig. 2a), the impression of his specimen may represent an undulation of the interior shell surface, which is frequently present, or damage by exfoliation of part of the surface.

Because most specimens are gaping and/or displaced, determination of the presence or absence of a byssal gape is difficult. If present the byssal gape is slight. There are two indefinite sinuosities, either of which could be a gape: one directly below the anterior ear (the most probable byssal gape) and the other in the anterior margin at about one eighth of height below dorsal margin and at the end of a faint sulcus that extends ventrally and slightly posteriorly from just anterior to the umbone. The sulcus is not visible on many specimens. Several specimens retain some fibrous lustrous ligament material, the inner layer of Trueman (1954), in the pits.

The construction of the shell is similar to that of *Pinctada martensii* (Wada, 1961). The outer prismatic layer is generally recrystallized to a grayish translucent, coarsely crystalline state. Some specimens retain the prismatic structure. The pearly nacreous

inner layer shows the growth spirals characteristic of nacre.

MATERIAL. Approximately 5000 specimens as individuals and in selected blocks and concretions. Abundant in *Limopsis-Pseudoptera* Assemblage Zone (96.6%) but very rare in all other assemblage zones, from which only 134 specimens were collected.

Occurrence. Pseudoptera subtortuosa occurs in the Limopsis-Pseudoptera Assemblage Zone as masses of closely packed, chaotically oriented or aligned specimens (Pl. 11, figs. 6-9), either by itself or associated with the other codominants Limopsis striatopunctatus and/or Corbula inornata. Single specimens are rare in Limopsis associations. The species occurs as isolated specimens in concretions of the other assemblage zones. Most of the specimens are bivalved, articulated and slightly gaping, although a considerable number have the valves displaced varying distances. Articulated valves dominate also in the other assemblage zones where the ratio of disarticulated to articulated specimens is 1:4.6, 1:2.1 and 1:1.2 for the Lower nicolleti Assemblage zone, Protocardia-Oxytoma Assemblage Zone and Timber Lake Member occurrences. Though it is difficult to dismember concretions to obtain quantitative data, single valves are numerically inconspicuous.

Large specimens, those with an oblique length greater than 60 mm, are dominant in the Lower *nicolleti* and *Protocardia-Oxytoma* assemblage zones, the ratio of small to large specimens being 1:3.7 and 1:6.3 respectively; yet the presence of small specimens indicates that the species was able to exist in the apparently unfavorable conditions pre-

vailing at the time.

The restriction to individual concretions of specimens of a limited range of size classes is common at many localities in the Limopsis-Pseudoptera Assemblage Zone. Repetitive size classes have the oblique length falling within the ranges of approximately 5 to 15 mm (A1150; Pl. 11, fig. 7), 20 to 30 mm (A1141; Pl. 11, fig. 9), 35 to 50 mm (A1170; Pl. 11, fig. 8), 60 to 80 mm (A1172, A1309; Pl. 11, fig. 6) and greater than 90 mm (A600). Most specimens greater than 90 mm occur as isolated individuals in associations dominated by other species or with abundant specimens of a smaller size class. Some concretions contain more than one range of size classes, and these are generally well differentiated into local "clusters" within a concretion (Pl. 11, fig. 9), although some mixing may occur around the contacts of the clusters. In other cases larger specimens are scattered through those of a numerically dominant smaller size range (Pl. 11, fig. 6). Qualitative observations and concretion counts indicate that associations of large specimens are significantly less frequent than those with small size range of less than 50 mm oblique length. Concretionary masses of large specimens occur mostly in the upper part of the Lower nicolleti Assemblage Zone, where Drepanochilus associations are dominant, and in the Limopsis-Pseudoptera Assemblage Zone along the Grand River. Because of the difficulty in extracting sufficient complete specimens to provide measurements for the construction of size-class histograms, the size groupings as listed above are shown pictorially. If we accept the hypothesis that the restricted ranges of size classes represent different spatfalls, the dominance of small specimens is compatible with the common high mortality rate of young bivalves.

Comparisons. Meek (1876) listed two species of Gervillia from the Western Interior: subtortuosa Meek & Hayden from "three hundred miles above Fort Union, on the Missouri River; in the Fort Pierre Group", and recta Meek & Hayden from "Deer Creek, near North Platte; in the lower part of the Fox Hills". The type specimens are from localities outside the type area of the Fox Hills and from slightly different stratigraphic positions, and although the morphology of the anterior end of the ligament is unknown, they match specimens from the type Fox Hills in all other internal and external aspects and are undoubtedly conspecific and congeneric. The degree of twisting of subtortuosa is extremely variable.

Pseudoptera propleura (Meek, 1873), from the lower part of the Frontier Formation (Stanton, 1893; Eardley, 1944), Cenomanian-Turonian, Coalville, Utah, is subquadrangular rather than prosocline and has a strong oblique plica along the posterodorsal surface. Additional specimens are required to prove its generic status. The species from the Woodbine Formation (Cenomanian), Texas and P. securiformis, Stephenson (1956), from the Eutaw Formation, Alabama-Georgia differ from subtortuosa in being subtrigonal (correlated with their small H/L ratio and very prosoclinal form), in having more distinct external radial costation, and in the presence on some specimens of a strong lateral tooth. Whiteaves (1885, p. 36) considered that his Gervillia recta var. borealis differed from the type only by "its much larger size" and "the greater length of its posterior wing", and was possibly not distinct enough "to be called a variety". His figured specimens can be matched by specimens in the Yale collections and are undoubtedly conspecific. The shape and anterodorsal projections of the steinkern of Pteria parkensis White (1876; 1879b, Pl. 3, fig. 3a; USNM 8074) suggest that it is a Phelopteria.

PHELOPTERIA

AUTHOR. Stephenson, 1952, p. 68.

Type Species. By original designation, *Pteria? dalli* Stephenson (1936, p. 389–390, Pl. 3, figs. 19–20), dredged from Banquerau Bank, Nova Scotia, Upper Campanian-Maestrichtian, and Woodbine Formation, Texas, Cenomanian (Stephenson, 1952, p. 68–70, Pl. 14, figs. 4–14).

Discussion. A detailed examination of all species included in the genus is required before an adequate diagnosis is prepared. Stephenson noted that Phelopteria is externally very similar to Pteria Scopoli but differed from the type species, Pteria hirundo (Linnaeus), by lacking the long posterior ear and by having a shorter and less pointed anterior ear. These are not of significance, for the species to be described below, Phelopteria linguaeformis (Evans & Shumard), may have a long, narrow, pointed or a short, stunted posterior ear, and its anterior ear may be long or short, pointed or rounded. The diagnostic feature, emphasized by Stephenson, is the presence of multivincular, triangular, ligament pits during the "juvenile stage" which may merge into one long shallow pit on large specimens. Small and large specimens of linguaeformis may have two to five pits and, although up to three pits may fuse during growth, fusion is less complete than for specimens of dalli, which may be extreme in this tendency. The small specimens of dalli figured by Stephenson (1952, Pl. 14, fig. 10) have ligament areas comparable in all respects to similar-sized specimens of linguaeformis. Other features of linguaeformis that might be diagnostic at the generic level are the lack of a byssal notch (a byssal gape appears to be present) under the posterior ear of the right valve, and the discordance in shape of the posterior adductor muscles discussed below.

The *Pteria*-like shape of *Phelopteria* and the presence of serial ligament pits suggest that the genus might best be classed in the family Bakevelliidae King (Cox, 1954, p. 47).

Phelopteria linguaeformis (Evans & Shumard) (Plate 12, figs. 3–10; Plate 13, figs. 1–12)

Avicula linguaeformis Evans & Shumard, 1854, p. 163. Meek, 1859, p. 183, Pl. 1, fig. 6. Stanton, 1899, p. 637.

Avicula subgibbosa Meek & Hayden, 1860a, p. 180.

Pteria linguiformis (Evans & Shumard). Meek, 1864a, p. 9. Meek, 1876, p. 32, Pl. 16, figs. 1a-d. White, 1879a, p. 180, 197, 205. Whitfield, 1880, p. 384, Pl. 7, figs. 2, 4. Whiteaves, 1885, p. 31. Stanton, 1920, p. 24, Pl. 3, fig. 1. Cvancara, 1966, p. 319, Pl. 3, fig. 7.

Pteria subgibbosa (Meek & Hayden). Meek, 1864a, p. 9.

Pteria linguiformis var. subgibbosa (Meek & Hayden). Meek, 1876, p. 33, Pl. 28, fig. 12. Whiteaves, 1889, p. 74.

[?]Pteria linguaeformis var. borealis Warren, 1930, p. 64, Pl. 4, figs. 4, 5.

[?]Pteria? linguaeformis (Evans & Shumard). Stephenson, 1941, p. 102, Pl. 12, figs. 7, 8.

DESCRIPTION. Length of the left valve of measured specimens 6.2 to 62.4 mm, slightly inequivalve but appearing to be strongly inequivalve, inequilateral, moderately inflated, maximum inflation in dorsal half. Umbones prosogyrous, not prominent, project slightly above dorsal margin. Shape of valves variable, pterioid, differences in the height to length ratio and the angle 9 (measure of prosoclinality) resulting in very to moderately prosoclinal high to low forms (Figure 11), with long tapering to relatively short blunt posterior ears and small narrow tapering or wide rounded anterior ears of variable length. Posterior ears and the anterior ear of left valve not delimited from disc of shell. Anterior ear of right valve delimited by a weakly or strongly impressed narrow sulcus, no byssal notch at end of sulcus, but shell margin apparently with a byssal gape. Measurements made on the outline of the inner shell layer for height, anterior length, oblique length, length of dorsal margin, inflation and length from anterior ear to base of posterior ear (IL) are, respectively, 71.8 to 94.9 (N = 30, μ = 84.3%), 19.8 to 34.8 (N = 29, μ = 25.1%), 108.3 to 122.7 (N = 31, μ = 116.1%), 94.2 to 96.6 (N = 30, μ = 95.4%), 11.1 to 20 $(N = 30, \mu = 15.1\%)$ and 63.2 to 96.5 $(N = 28, \mu = 78.4\%)$ percent of the length of the left valve, and 68.8 to 94.5 (N = 36, μ = 79.3%), 18.9 to 35.2 (N = 36, $\mu = 27.5\%$), 104.6 to 126.6 (N = 36, $\mu = 114.2\%$), 89.5 to 110 (N = 12, $\mu = 101.2\%$), 8.3 to 20.2 (N = 30, μ = 12.1%) and 71.8 to 98.6 (N = 35, μ = 86%) percent of the length (4.8 to 50.9 mm) of the right valve. The angle 9 ranged from 31 to 50 degrees. Shell ornamented with fine growth lamellae, widely spaced on disc of shell, closely packed and more prominent on ears and along dorsal margin, and with irregular shallow growth corrugations which are more numerous ventrally on large specimens.

Ligament area extends the length of dorsal margin, tapers posteriorly rapidly, widest under umbones, inclined at about 60 degrees to the vertical, marked by fine longitudinal striae. Part of ligament between umbone and base of the posterior ear with two to five impressed, steep-sided ligament pits on large specimens, pits initially triangular, tending to become parallel-sided with growth and generally to fuse, so reducing the number of pits by one to three. Left valve with a weak to strong lamellar or nodular tooth under margin of ligament anterior to umbone, bordered on both sides by sockets for reception of two weak nodular teeth, the posterior or anterior of which may be the stronger, on the right valve. Each valve has, immediately below the hinge and above the adductor scar, a short linear lateral tooth of variable strength. The ventral margin of the socket on the right valve for the reception of the lateral of the left valve tends to be thickened and to

simulate a second lateral.

Monomyarian, posterior adductor insertion area large, situated behind mid-height on left valve, slightly lower on right valve, marked by growth lines that parallel the posterior and anterior margins. Adductor insertion area of left valve subquadrangular, with a deep concavity in dorsal margin and sometimes minor ones in lateral margins, that of right valve pear-shaped with the anteroventral margin more projecting and larger, tapering posterodorsally. Pallial line with 11 to 20 small discrete oval to linear coalesced inser-

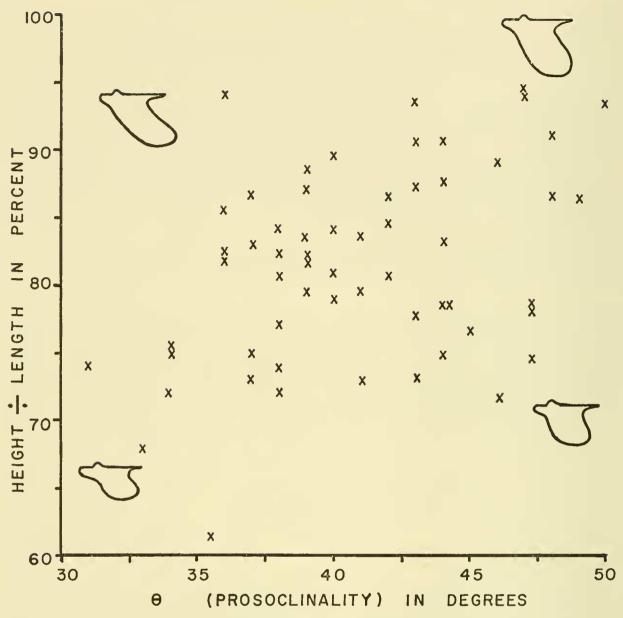


Fig. 11. Scatter diagram of prosoclinality (Θ in degrees) plotted against form ratio (height expressed as percentage of length), showing large variation of shape of *Phelopteria linguaeformis*. N = 58. (From many concretions.)

tions, most impressed dorsally, extending in a loop from the posteroventral margin of the adductor into the umbone. The posteroventral pallial insertion is sometimes fused to the adductor. Above the adductor two to four small insertion pits extend anterodorsally to the margin of the ligament where one to three insertions may occur. Two deeply impressed insertions (pedal elevator) are sited in the umbone, one on the lower posterior flank, and the other, a very deeply impressed insertion area, at the base of the anterior ear. Tip of umbonal cavity, especially the posterodorsal surface, generally has two to five small oval or linear coalesced insertions, sometimes in a horseshoe pattern.

Ostracum very thin, up to 0.8 mm thick on main disc of shell for large specimens, thicker in the ligament area, consisting of a very thin outer prismatic layer that projects beyond the inner layer (Pl. 12, fig. 8), and thick only in the vicinity of the anterior ear where layers are repetitive, and an inner nacreous layer five to six times thicker than the outer layer. Outer surface of inner layer with faint radial costae, inner surface with radial costae, especially ventrally.

Types. Location of Evans and Shumard's original collection unknown. Type locality: Sage Creek, South Dakota. Stratigraphic position: Pierre Shale, Maestrichtian. Lectotype of Avicula subgibbosa, USNM 461, by subsequent designation of Meek (1876, in

caption to Pl. 28, fig. 12), a left valve steinkern with shell remaining on the anterior ear, L = 38.5, H = 36.8, OL = 48.6 and AL = 11.7 mm. Type locality: Long Lake, North Dakota. Stratigraphic position: Fox Hills Formation, Timber Lake Member.

Types held at YPM are: hypotypes YPM 24056-74, and 24607A.

Discussion. The outer shell margin may extend for a considerable distance posteroventrally (Pl. 12, fig. 8) and measurements made on the inner shell outline may have little relation to the true shape of the specimen. Nevertheless, for the left valve the outline generally corresponds closely to that of the inner layer and, as steinkerns are all that are usually available, these have to be measured.

Measurements made on one specimen (YPM 24064; Pl. 12, fig. 8) indicate that it is approximately equivalve and that the left valve is only slightly more inflated than the right valve. The relative dimensions of the valves, based on outline of the inner shell, are as follows: Length, height, oblique length, inflation and length from tip of anterior ear to base of posterior ear (IL) of the right valve are, respectively, 79.3 to 86.2 (N = 6, $\mu = 83\%$), 69 to 83.7 (N = 5, $\mu = 76.8\%$), 77.1 to 85.8 (N = 6, $\mu = 82.5\%$), 60.7 to 85.2 (N = 6, $\mu = 71.6\%$) and 91.9 to 98.4 (N = 4, $\mu = 96.2\%$) percent of comparable left valve measurements for articulated specimens. The angle Θ is difficult to measure and the values given above are approximate and may have an error of up to 5 degrees.

Pearly fibrous inner ligament material is preserved in the ligament pits of many specimens at Loc. 83 (A724). The fusion of anterior ligament pits on many moderate-size specimens and the common consequent reduction to two pits (Pl. 13, fig. 10) suggest that on some large specimens fusion could result in one long pit.

MATERIAL. About 1800 specimens as individuals and in selected blocks and concretions.

Occurrence. This species is present in all major assemblage zones of the Timber Lake Member but is common only in the marine facies of the member. Twenty-one point eight percent were collected from the Trail City Member, 90 (5.3%) from one assemblage (A1328) in the Limopsis-Pseudoptera Assemblage Zone. Five point one percent were collected from the Tancredia-Ophiomorpha Biofacies of the Timber Lake Member. The species occurred as scattered specimens except at Loc. 83 where it is associated with Ostrea translucida as a codominant in small clumps. In the assemblage zones of the Timber Lake Member linguaeformis is present as scattered specimens, as a codominant with one or two other species or, rarely, as a dominant. The common assemblages are Phelopteria, Phelopteria-Oxytoma, Phelopteria-Ostrea and Protocardia-Phelopteria.

Articulated valves dominate the occurrences in the Trail City Member. Breakage and disarticulation of valves is common in the Timber Lake Member which is compatible with the higher energy environment. There is, however, great diversity, and where *P. linguaeformis* is a dominant in an assemblage, articulated specimens and/or approximately equal numbers of left and right valves are present. This suggests minor transport or sublevation. The restriction of size classes is not as marked for this species as for others. Nevertheless, in several collections (A478, A348, A631) the oblique length of specimens falls in two or more of four approximately defined groups with little overlap: less than 10 mm, 13 to 20, 25 to 35, greater than 35 mm.

Specimens considered to be conspecific with or closely related to *linguaeformis* are frequently recorded in the Upper Cretaceous of the Western Interior (Fisher and others, 1960; Stanton, 1893, p. 74; Warren, 1930; Whiteaves, 1885), and in the Cannonball Formation (Paleocene) of North Dakota (Stanton, 1920). Stephenson (1941, p. 102), recorded it from the Navarro Group, Texas.

Comparisons. The generic placing of many Upper Cretaceous specimens included under various "Pteria" species by many authors is uncertain and requires a knowledge of the internal characteristics, especially the morphology of the ligament. The gross external similarity of Stephenson's (1952) genera Panis and Phelopteria to Pseudoptera, Pteria

and some gervilloid genera indicates the difficulty of classifying species based on external form alone. All the specimens representing the species listed in the synonymy above are indistinguishable externally from specimens of linguaeformis from the type Fox Hills. Yet, because the ligament areas are unknown, the synonymy given above is considered tentative. Specific identity of many poorly preserved and incomplete Pteria-like specimens from Upper Cretaceous sequences of the Western Interior and Gulf and Atlantic

Coastal Plains is considered to be unproven.

The status of Pteria petrosa (Conrad), often considered (Wade, 1926; Weller, 1907; Gardner, 1916) conspecific with linguaeformis, must await adequate well-preserved samples (see also Stephenson, 1923, p. 131). Stephenson's (1923, Pl. 27, figs. 5, 6; USNM 31533) specimen from Snow Hill has a characteristic Phelopteria hinge. Stanton (1893) thought that some specimens of Avicula gastrodes Meek (1873) from the Frontier Formation, Coalville, Utah were "scarcely distinguishable from . . . Avicula linguaeformis". Some extremely small specimens in his collection (USNM 22866) do resemble comparable-size specimens of linguaeformis, but the large specimens are stouter, more rectangular, have a longer and more massive anterior ear and reach a greater size. Avicula gastrodes is probably a distinct species. Phelopteria dalli, the type species, differs from linguaeformis by attaining a much larger size (IL = 65 and 44 mm maximum respectively) and the stronger tendency for the multivincular pits to fuse, and Stephenson's (1952, USNM 105173-6) specimens from the Woodbine Formation, Texas consistently have a much stronger tooth on the valve and a more rectangular and less prosoclinal shape.

Gervillia rostrata (Sowerby; Woods, 1905, p. 83, Pl. 11, figs. 12-23) closely resembles

linguaeformis in shape and ligament characteristics and is probably a Phelopteria.

MYTILACEA

MODIOLUS

AUTHOR. Lamarck, 1799, p. 87.

Type Species. By absolute tautonymy under the Plenary Powers (ICZN Opinion 325, 1955, v. 9), Mytilus modiolus Linnaeus (1758, v. 1, p. 706), Recent, circumboreal.

Modiolus meeki (Evans & Shumard) (Plate 16, figs. 1, 3, 5–11)

Mytilus meekii Evans & Shumard, 1857, p. 40.

Description. Length of specimens 4.9 to 28.3 mm, equivalve, strongly inequilateral, moderately inflated. Shape rather consistent, elongated subquadrangular, subcylindrical in cross-section. Anterodorsal margin straight, inclined at 10 to 20 degrees to the line through the ventral extremities, posterodorsal angulation not marked, posteroventral angulation acute, ventral margin straight or weakly concave when a broad faint sulcus is present, and anterior margin prominent, broadly rounded, projecting in front of umbones. Height, anterior length and half width, respectively, 45.1 to 64.1 (N = 36, μ = 55.9%), 8.5 to 14.5 (N = 35, μ = 10.8%) and 15 to 25.3 (N = 36, μ = 18.8%) percent of length. Inflation rather uniform all over shell except for a posterodorsal and a less marked anteroventral taper. Maximum inflation along an umbonal to posteroventral angulation. Umbones prominent, project strongly above dorsal margin, incurved and prosogyrous.

Shell with fine concentric growth striae and plicae, the plicae with a short, steeply inclined or overhanging face pointing toward umbones. Plicae are prominent only on small specimens. Nymph prominent, resilial ridge fine, extends for about three quarters of the length of the straight anterodorsal margin and defines a narrow internal ligamental area. Hinge under umbones unknown, apparently typical of the genus. Muscle insertion areas weakly impressed, especially the posterior, heteromyarian. Anterior adductor small, elliptical, with a concave posterodorsal margin, situated below umbones in dorsal part of anterior margin. Posterior adductor subelliptical, its base situated about one third of height above ventral margin, continuous with a narrow, elongated posterior retractor that extends up to under the posterior end of nymph. Anterior retractor unknown. Pallial line continuous, relatively wide.

Ostracum very thin, less than 0.2 mm thick, of two layers. A thin outer translucent layer, either homogeneous or weakly prismatic, and an inner lamellar layer of subparallel sheets. Outer surface of inner layer with fine radial costae.

Types. Location of Evans and Shumard's specimens unknown. Type locality: Moreau River, South Dakota. Stratigraphic position: Fox Hills Formation, probably from *Protocardia-Oxytoma* Assemblage Zone.

Types held at YPM are: hypotypes YPM 24106-13.

Discussion. The measurements were made on steinkerns but, because of the thinness of the shell, they closely approximate the external dimensions. As the thin posterodorsal margin is most likely to be incomplete the height to length percentage may be low. Some specimens retain pearly, fibrous inner ligament layer.

MATERIAL. 158 specimens, 80 percent bivalved.

Occurrence. The species is rare and was collected from only 19 concretions. It is virtually restricted to the *Protocardia-Oxytoma* Assemblage Zone with rare specimens from the *Limopsis-Pseudoptera* Assemblage Zone and the marine biofacies of the Timber Lake Member, and one specimen from the *Tancredia-Ophiomorpha* Biofacies (Loc. 83). Eighty-seven percent came from the *Protocardia-Oxytoma* Assemblage Zone, all but eight specimens from three concretions. At Loc. 233 meeki was a codominant with *Protocardia* and *Oxytoma* in one concretion (A1008) and common in another (A1005), and at Loc. 191 it was a codominant with *Protocardia* in A567. Of the remainder, 7.5 percent come from the *Cucullaea* Assemblage Zone. The dominance of small sizes is notable. The occurrence of two specimens 50 percent larger than any other indicates that most are juveniles.

There are few records of this species from Upper Cretaceous sequences in the Western Interior. Griffitts (1949) recorded it in the Rocky Ridge Sandstone Member of the Hygiene zone, Pierre Shale, Colorado, and Robinson and others (1959) found it in the Pierre Shale west of the Black Hills. These should be reviewed (see below).

Comparisons. Soot-Ryen (1955, p. 58) has pointed out the difficulty of classifying young specimens in a species. Some recent species, for example M. americanus (Leach), show an allopatric growth trend, the small juveniles being subcylindrical, like M. meeki, and the adults more typically modiolid with a broad compressed posterodorsal margin and so closely resembling galpinianus (Evans & Shumard). M. meeki is quite distinct from galpinianus as is shown by many morphological features, the occurrence of one large specimen with similar characteristics to the small and the fact that recent species with inflated umbones and anterior retain these through life. M. galpinianus differs from meeki by its curved anterodorsal margin which is inclined at 35 to 50 degrees to the line through the anterior and posterior ventral extremities, the compressed umbones are subterminal, project only slightly above the dorsal margin of the shell and are below that of steinkerns, umbones are not incurved, the line of maximum inflation is situated

further ventrally, is more curved and fades before reaching the ventral margin, the anterior end below the umbone is compressed and this makes the angulation more distinct anteriorly, its shell is thicker, the muscle scar pattern, especially the anterior adductor and pedal retractor, is significantly more impressed on specimens of comparable size, the base of the posterior adductor is situated higher, the ornamentation lacks the regular sharp growth costae of *meeki*, and the species probably grows to a larger size.

Evans and Shumard described two species of Modiolus, meeki and galpinianus, from the region of Moreau River. In their original description of meeki they stated that it can be "readily distinguished from galpinianus". The common species in the Fox Hills best fits their description of meeki and differs from the rarer galpinianus by the characters they stressed. Unfortunately the lack of types prevents positive identification. The specimens (USNM 313) from the Yellowstone River described by Meek (in Meek and Hayden, 1860b; 1876) and placed in meeki are conspecific with galpinianus (as conceived here) from the type Fox Hills. As two species matching Evans and Shumard's original descriptions can be clearly recognized, and as Meek's meeki and galpinianus (USNM 446) are conspecific, the names are here used in what is believed to be the original concepts. Identifications based on Meek's concept and figures should be revised.

Modiolus uddeni (Stephenson, 1941), Navarro Group, Texas most closely resembles meeki and differs in being less inflated and cylindrical, with a narrower posterior end and fine regular concentric plicae over most of the shell (Pl. 16, figs. 2, 4).

Modiolus galpinianus (Evans & Shumard) (Plate 16, figs. 12–14; Plate 17, figs. 1–3)

Mytilus galpinianus Evans & Shumard, 1854, p. 164. Meek & Hayden, 1860b, p. 427. Modiola meeki (Evans & Shumard). Meek & Hayden, 1860b, p. 427. Volsella galpiniana (Evans & Shumard). Meek, 1876, p. 73, Pl. 15, figs. 7a,b. Volsella meeki (Evans & Shumard). Meek, 1876, p. 72, Pl. 15, figs. 3a-c. [?]Modiolus silentiensis McLearn, 1926, p. 125, Pl. 23, figs. 3, 4. [?]Modiolus wrighti Warren, 1934, p. 87, Pl. 2, fig. 2. [?]Volsella wrighti (Warren). Landes, 1940, p. 144. [?]Volsella anomala Landes, 1940, p. 142, Pl. 3, figs. 7, 8.

Description. Length of specimens 15.3 to 37.1 mm, equivalve, strongly inequilateral, moderately inflated. Shape arcuate subtrigonal, with greatest height about posterior third. Anterodorsal margin convex, inclined at 35 to 50 degrees to the line through the ventral extremities, continues as a wide curve to meet sinuous ventral margin. Anterior margin slightly projecting, weakly convex. Height, anterior length and half width, respectively, 41.6 to 58.6 (N = 10, μ = 51.5%), 1.9 to 10.2 (N = 10, μ = 6.9%) and 13.1 to 19.3 (N = 10, μ = 16.8%) percent of length. Umbones subterminal, compressed, not prominent. For other details see "Comparisons" under meeki above.

Shell with fine growth striae, irregular round-topped concentric costae and growth depressions. Ligamental area as for *meeki*, and hinge like present-day species with a weak tooth at the end of anterior margin. Muscle insertion areas strongly impressed, anisomyarian. Anterior adductor relatively large, situated along anterior margin, arcuate with internal margin concave and notched. Posterior insertion area comma-shaped, situated above mid-height, consisting of a large, oval posterior adductor fused to a narrow arched posterior pedal retractor that extends to under posterior end of nymph. Anterior pedal insertion elliptical, in tip of umbone, relatively large and deeply impressed. Between anterior adductor and retractor is a small impressed oval insertion with two to four very small pits on either side. Pallial line continuous, prominent.

Ostracum up to 1.1 mm thick, layering as for meeki.

Discussion. The measurements were made on five each of shells and steinkerns. The shells gave consistently higher height to length percentages and a more terminal position to the

umbones (Pl. 16, fig. 14). The range for the latter of 1.9 to 4.6 percent of length is more accurate, but the steinkern data (5.1 to 11.5%) are included for comparison with the steinkerns of meeki. The mean percentage for height might be one percent too low. The possession of a small prominent muscle insertion area between the anterior adductor and retractor is characteristic of Arcuatula (Jousseaume) Lamy (1919). Anterior adductor insertion areas of similar size, and notching of posterior margin and costation occur on species of Modiolus and Arcuatula. Soot-Ryen (1955, p. 56) noted that other features diagnostic of Arcuatula were the radial sculpture, crenulated anterior margin, weak nymph and narrow ligament. M. galpinianus lacks radial sculpture, has a relatively prominent ligament and nymph and is best classed in Modiolus.

Types. Whereabouts of original specimens unknown. Type locality: "Fox Hills", South Dakota. Stratigraphic position: probably Fox Hills Formation.

Types held at YPM are: hypotypes YPM 24117-20, 24698.

MATERIAL. 18 specimens; one articulated, and 17 single valves.

Occurrence. The species occurs in the Colgate lithofacies, Tancredia-Ophiomorpha Biofacies, in the shallower water phase of the marine biofacies of the Timber Lake Member to the northeast of the Moreau River, and in the Protocardia-Oxytoma Assemblage Zone, Trail City Member. Modiolus galpinianus was associated with an articulated specimen of meeki at Loc. 83, Tancredia-Ophiomorpha Biofacies. The otherwise mutually exclusive distribution of the two species is another factor favoring specific separation.

Comparisons. Features characterizing galpinianus are enumerated above under meeki. Evans and Shumard (1854) based their description on specimens from the "Fox Hills, Nebraska". Except for the mention of prominent umbones, which can be interpreted in several ways, their description matches the concept of the species held by Meek and writer. Meek (1876) was the first to figure specimens, yet by his listing of galpinianus under meeki (Meek and Hayden, 1860b, p. 427) he at one time apparently considered the two species to be synonymous.

The specimens of M. silentiensis figured by McLearn appear to be juveniles of galpinianus (cf. Pl. 16, fig. 12). The features used by Landes (1940, p. 144–145) to distinguish his specimens of wrighti also separate galpinianus from meeki. Identification of wrighti with galpinianus is reinforced by Landes' recognition of specimens gradational to galpinianus and the presence of weakly arcuate specimens at Loc. 97, Colgate Member. Volsella anomala Landes is probably a large specimen of galpinianus.

Warren's wrighti resembles galpinianus but may be specifically indeterminable.

Modiolus aff. M. attenuatus (Meek & Hayden) (Plate 17, fig. 4)

Mytilus attenuatus Meek & Hayden, 1856a, p. 86.

Modiola attenuata (Meek & Hayden). Meek & Hayden, 1860b, p. 427. Meek, 1864a, p. 11. Whiteaves, 1885, p. 36.

Volsella attenuata (Meek & Hayden). Meek, 1876, p. 74, Pl. 28, figs. 8a, b. Landes, 1940, p. 143.

[?] Modiolus attenuatus (Meek & Hayden). Fisher and others, 1960, p. 33.

[?] Adula sp. Cvancara, 1966, p. 316, Pl. 3, figs. 15–18.

Discussion. Two specimens, one bivalved (YPM 24114, 24741), from three localities (34 (A341), 92 (A920), 210 (A450)) in the *Cucullaea* Assemblage Zone, Timber Lake Member, closely fit descriptions of *attenuatus*. One is incomplete posteroventrally, and the anterior end of the other is crushed and distorted by compaction. Both are elongated with a low height to length ratio (c.30 to 40%), compressed with a projecting, rounded, com-

pressed anterior extremity and, compared to galpinianus, with subterminal relatively prominent umbones that project above the dorsal margin as for *meeki*. The anterior adductor insertion area is visible on the smallest (YPM 24741) and in its position, shape and degree of impression resembles that of *meeki*.

Landes (1940, p. 143) has given the best description and discussion of this species and his work indicates that the species is valid. As noted by Meek (1876) the distinctive characters, exclusive of shape, suggest a resemblance to meeki. Yet judging by growth lines and Landes' observations, the shape is very different even for juveniles. The anterior end is narrower, more pointed and compressed, the ventral margin is convex and the umbonal angulation is insignificant. The specimens of Adula sp. described by Cvancara (1966) closely resemble the poor specimens of attenuatus.

Modiolus aff. attenuatus is rare in Upper Cretaceous sequences of the Western Interior. It is abundant only through some 50 feet of the Bearpaw Formation in the Manyberries section, Southern Alberta (Russell, 1940; Landes, 1940). The type specimens were collected from the vicinity of the Moreau Trading Post, within the type area of the Fox Hills Formation, probably from the Timber Lake Member. The lectotype, USNM 486, by subsequent designation of Meek (1876, in caption to Pl. 28, fig. 8a; greatly idealized), a bivalved gaping steinkern, the right valve crushed anteriorly and its umbone incomplete, L = c.47.3, H = c.15.6, ½ W = c.4.5 mm, closely matches our specimens and appears to be distinct from meeki and galpinianus.

BRACHIDONTES

Author. Swainson, 1840, p. 384.

Type Species. By monotypy, Modiola sulcata Lamarck (1819, p. 113), Recent, Indian Ocean.

Brachidontes? sp. indet. (Plate 17, fig. 5)

Discussion. Two poorly preserved small specimens (YPM 24121), a left valve steinkern and a right valve mould, and many shell fragments, possibly attributable to *Brachidontes*, were collected from the *Crassostrea subtrigonalis* shell bed at Loc. 170, Colgate lithofacies. The shells, each about 15 mm long, have about 28 (4 per mm) costae around the posterior margin between the dorsal and ventral angulations, and finer costae anterior to these points. The costae are round topped, steep sided and bifurcate once, although those on the posterodorsal flank tend to undergo a double bifurcation. The costation resembles that of *Arcuatula demissa* (Dillwyn) (see Soot-Ryen, 1955). Details of the hinge are required to ascertain the true generic position.

In general size, shape and costation the specimens resemble *B. regularis* White (1878; 1883c, Pl. 25, fig. 3a) and also *Arcuatula schallerensis* (Stanton, 1920, p. 25; Cvancara, 1966, p. 314, Pl. 3, figs. 6, 12–14) to which it should be compared very closely.

CRENELLA

Author. Brown, 1827, Pl. 31, figs. 12-14.

Type Species. By monotypy, Mytilus decussatus Montagu (1808, p. 69), Recent, Boreal seas.

Crenella elegantula Meek & Hayden (Plate 17, figs. 6–11)

Crenella elegantula Meek & Hayden, 1861, p. 441. Meek, 1864a, p. 11. Meek, 1876, p. 75-76, Pl. 28, figs. 6a-c. White, 1879a, p. 181. Landes, 1940, p. 147. Kellum, 1962, p. 53.

[?] Crenella elongata Stanton, 1920, p. 25, Pl. 2, figs. 8a,b. (= stantoni Finlay, 1927, p. 525, non elongata Hutton, 1873, p. 25).

[?]C. cedrensis Stanton, 1920, p. 25, Pl. 2, figs. 9a-c. Cvancara, 1966, p. 312, Pl. 3, figs. 3, 4.

[?] C. subcircularis Stephenson, 1952, p. 86, Pl. 19, figs. 15, 16. [?] C. microstriata Stephenson, 1955, p. 114, Pl. 17, figs. 7–10.

[?] C. elegantula Meek & Hayden. Weller, 1907, p. 115, Pl. 56, fig. 6. Gardner, 1916, p. 625, Pl. 36, fig. 19. Richards, 1958, p. 156, Pl. 25, fig. 10.

[?] C. stantoni Finlay. Cvancara, 1966, p. 313, Pl. 3, figs. 9-11.

Description. Length of specimens 1.8 to 24.6 mm, equivalve, strongly inequilateral, moderately to strongly inflated with maximum inflation in dorsal third of height at about anterior third of length. Small specimens suboval, but with growth the height to length ratio decreases and the shell becomes subrectangular (Fig. 12). Anterodorsal margin above ligament straight or slightly convex, anteroventral margin rounded, sometimes weakly projecting anteriorly and with an angulation. Height and width of one valve, respectively, 58.7 to 98.0 (N = 83, μ = 77.3%) and 19.5 to 37.4 (N = 83, μ = 29.6) percent of length. Umbones terminal, at about dorsal third of height, prominent, incurved, prosogyrous, and project 1.7 to 8.4 (N = 77, μ = 5.2%) percent of length beyond the anterior margin.

Prodissoconch smooth, sharply delimited from main part of shell, I to 1.5 mm long. Disc of shell ornamented by fine round-topped and steep-sided costae, wider than interspaces, 8 to 15 per mm at a length of 10 mm. Costae increase in number mostly by gemmation and secondarily by intercalation, and remain rather uniform in size. Costae crossed by fine growth striae and lamellae and by irregular growth-pause depressions of variable prominence. Ligament internal, 14.3 to 26.6 (N = 25, μ = 21.7%) percent of length, narrow, with a thin ventral resilial ridge. Anterior end of ligament sunken between dorsal margin and the projecting, faintly striated, toothlike end of anterior margin. Muscle insertion areas unknown except for a weakly to moderately strong impressed small oval impression (?anterior pedal retractor) in umbone (Pl. 17, fig. 11).

Ostracum very thin, less than 1.5 mm thick, of two layers, a very thin outer translucent homogeneous layer and an inner subnacreous layer with lamellar structure. The inside of the shell has faint costae, especially ventrally, and the shell may tend to be plicate. Shell margins smooth or weakly crenulate and striate, particularly below the umbones.

Types. Lectotype of Crenella elegantula, USNM 1925, by subsequent designation of Meek (1876, in caption to Pl. 28, fig. 6a; idealized), a right valve steinkern with some inner shell, L=13.8, H=10.8, 1/2 W=4.2 mm. Type locality: Deer Creek, near North Platte, Wyoming. Stratigraphic position: Fox Hills Formation (Upper Cretaceous, Maestrichtian). Holotype of C. elongata Stanton, USNM 32396, by original designation, a poorly preserved right valve with some inner shell, L=23, H=14.5, 1/2 W=4.5 mm. Type locality: one mile south of Price, North Dakota. Stratigraphic position: Cannonball Formation (Paleocene). Holotype of C. subcircularis Stephenson, USNM 105286, by original designation, an articulated shell, L=5.9, H=5.2, W=4.4 mm. Type locality: Cornelius Creek, Grayson County, Texas, Loc. 165. Stratigraphic position: Templeton Member, Woodbine Formation (Cenomanian).

Types held at YPM are: hypotypes 24091–96.

Discussion. The thinness of the shell means that the measurements, although made on steinkerns or specimens with inner shell layer, should closely approximate the external

dimensions. Bernard (1898) and Fleming (1959) have also reported a decrease in height to length ratio with growth for recent species of *Crenella*. The large number of indeterminable valves recorded below is due to nonextraction or nonexcavation of specimens on blocks rather than to incompleteness of specimens.

MATERIAL. 288 specimens, mostly single valves.

Occurrence. Crenella elegantula is concentrated in the Trail City Member with 59.3 percent of the specimens coming from the Lower nicolleti Assemblage Zone and 22.2 percent from the Protocardia-Oxytoma Assemblage Zone. The remainder came from the Timber Lake Member, mostly from the Sphenodiscus (5.9%) concretion layer and Cucullaea Assemblage Zone. More than five specimens were present in only nine of 56 concretions. The species is a codominant with Discoscaphites in one assemblage (A547). It occurred as scattered specimens in all other cases. Single valves dominate.

Crenella elegantula is apparently rare in the Upper Cretaceous of the Western Interior. Robinson and others (1959) recorded it from the Pierre Shale, west of the Black Hills, and Kellum (1962) from the Fox Hills Formation, Niobrara County, Wyoming. Stanton (1920) described it, as C. elongata, from the Cannonball Formation (Paleocene), North Dakota.

Comparisons. The height to length percentage calculated from measurements quoted for specimens of elegantula or for specimens of species considered by several authors to resemble elegantula closely are plotted on Figure 12. All species have similar shape and the number of costae fall within the range of variation of elegantula. The plots suggest that C. elongata Stanton and C. subcircularis Stephenson are, and that microstriata most probably is conspecific with elegantula from the type Fox Hills. Stephenson (1955, p. 114) thought that microstriata, with 6 to 8 costae per mm (the holotype has 8 to 9) at the posterior margin of large specimens, had finer costation than elegantula, but the data suggest that the reverse may be the case for the latter has 8 to 15 per mm at 10 mm length with 2 to 4 less at the posterior margin of specimens longer than 15 mm. Compared to elegantula the specimens of cedrensis Stanton, microstriata, and one of Landes' specimens of elegantula have greater height to length percentage values. Weller (1907), Wade (1926) and Richards (1958) all refer Atlantic or Gulf Coastal Plain specimens to elegantula, although Stephenson (1955) considered Gardner's specimens to be closer to microstriata. Statistical treatment of samples, preferably from populations, is required before the specific status of these specimens is proved. Nevertheless, the plots suggest that the differences for height to length percentages may be phenotypic, except perhaps for cedrensis, and that the specimens may be conspecific with elegantula.

Crenella pterophora Warren (1926, Pl. 1, figs. 9, 9a; Univ. Alberta Ct. 300) is a modiolid or Brachidontes. Hinge and musculation details are required to ascertain its systematic position.

PECTINACEA

OXYTOMA

Author. Meek, 1864b, p. 39.

Type Species. By original designation, Avicula munsteri (Bronn, nomen nudum) Goldfuss (1836, p. 131, Pl. 118, figs. 2a-h), Middle Jurassic, Europe.

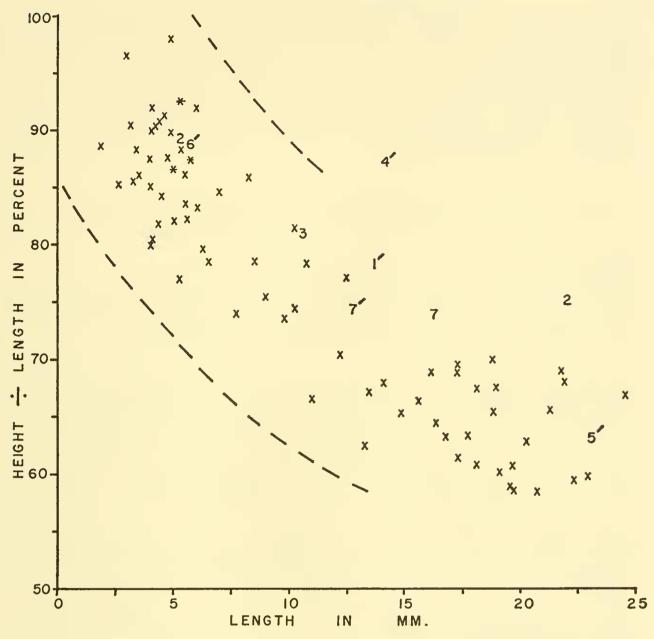


Fig. 12. Crenella elegantula. Scatter diagram of length plotted against form ratio (height expressed as percentage of length), showing greater elongation with increasing size. N = 74. * = >1 specimen. ' = holotype.

Numbers mark position of closely related species (remeasured where possible).

- 1. Crenella elegantula, holotype
- 2. C. elegantula. Landes, 1940
- 3. C. elegantula. Weller, 1907
- 4. C. cedrensis Stanton, 1920

- 5. C. elongata Stanton, 1920
- 6. C. subcircularis Stephenson, 1952
- 7. C. microstriata Stephenson, 1955

Subgenus HYPOXYTOMA

Author. Ichikawa, 1958, p. 164.

Type Species. By original designation, Avicula danica Ravn (1902), Maestrichtian, Europe.

Discussion. Ichikawa distinguished Hypoxytoma from Oxytoma sensu stricto by its relatively small size, presence of numerous primary costae of equal prominence, narrow interspaces between the costae, the general degeneration of costae in the umbonal region and the moderate incision of the byssal slot. The significance of these factors can be

evaluated only after a detailed revision of the species included in the genus. Hypoxytoma nebrascana (Evans & Shumard), described below, was included by Ichikawa in the subgenus. It grows to a relatively large size and the byssal notch is sometimes narrow and relatively incised. Yet it is characterized by numerous costae of equal strength and a smooth umbonal region. Ichikawa's subgenus is, therefore, tentatively accepted here.

It is significant that species placed in the subgenus are mainly from the Upper Cretaceous whereas typical Oxytoma is most numerous in the Upper Triassic to Lower Cretaceous. Ichikawa (1958) and Cox (1962) have shown that Oxytoma should be included in the superfamily Pectinacea.

Oxytoma (Hypoxytoma) nebrascana (Evans & Shumard) (Plate 13, figs. 13, 14; Plate 14, figs. 1–13; Plate 15, figs. 1–4)

Avicula nebrascana Evans & Shumard, 1857, p. 38. Meek, 1859, p. 183, Pl. 1, fig. 7.
Pteria nebrascana (Evans & Shumard). Meek, 1864a, p. 9. Kellum, 1962, p. 60, Pl. 2, figs. 7-11.
Pteria (Oxytoma) nebrascana (Evans & Shumard). Meek, 1876, p. 34-36, Pl. 16, figs. 3a-c; Pl. 28, fig. 11. White, 1879a, p. 180. Whitfield, 1880, p. 385-386, Pl. 7, fig. 4. Whiteaves, 1885, p. 31, 56, 79.
Oxytoma (Hypoxytoma) nebrascana (Evans & Shumard). Ichikawa, 1958, p. 164.

DESCRIPTION. Length of the left valve of measured specimens 4.2 to 29.6 mm, slightly inequivalve but appearing to be strongly inequivalve, inequilateral, inflation slight, shape of each valve moderately variable. Left valve subquadrangular to subtrapezoidal (Fig. 13), the anterior and posteroventral margins extending beyond dorsal margin for variable distances, weakly to strongly prosocline, the angle formed by the dorsal margin and a line between the umbone and the posteroventral extremity between 30 and 60 degrees. Height, anterior length, oblique length, length of dorsal margin and inflation are, respectively, 77.1 to 98.4 (N = 48, μ = 89.6%), 14.9 to 31.7 (N = 48, μ = 22%), 102 to 121.9 (N = 48, $\mu = 109.8\%$), 60.1 to 93.5 (N = 48, $\mu = 75\%$) and 6.7 to 16.1 (N = 38, $\mu = 11.3\%$) percent of the length. Maximum inflation at about one quarter of height below umbone, grading posterodorsally into a large, flat, pointed posterior ear which is mostly short but is sometimes attenuated. Anterior ear small, not or weakly delimited from main disc of shell, slightly to strongly convex (Pl. 14, fig. 1), its internal surface markedly thickened at the point of reflexion. Umbone prominent, projects above hinge line, slightly prosogyrous, strongly incurved. Prodissoconch and first 0.8 to 3.5 mm of umbone smooth; 37 to 48 primary radial costae appear over an interval of 1 to 3 mm, secondary costae intercalate at 4 to 7 mm and rapidly become equal to primary costae in strength, and on large specimens tertiary and rarely quaternary costae intercalate along the ventral margin over the ventral I to 6 mm, giving between 80 to 113 costae at the ventral margin of specimens greater than 15 mm length. The main disc of the shell has between 70 and 100 costae of equal prominence. Costae narrow, round-topped, steep-sided, and separated by flat-floored interspaces three to four times as wide. Costae most closely packed on anterior ear and at junction of posterior ear and main disc of shell. Number of costae on posterior ear variable, frequently of a low number. Costae tend to bend outward along anterior and posteroventral margins of large specimens. Ventral two thirds of large specimens is plicate. Concentric ornament of fine growth striae and rare more distinct growth pause depressions where the costae are frequently displaced relatively (Pl. 13, fig. 14).

Right valve mostly subquadrangular, slightly prosocline, the posteroventral margin sometimes elongated to give a stronger prosoclinal form. Valve fits inside left valve, the dorsal half convex, but a strong outward reflexion results in a very thin ventral border of outer shell layer continuing almost to the ventral margin of the left valve. Height, anterior length, oblique length, length of dorsal margin and inflation of the dorsal part of the right valve are, respectively, 80.6 to 111.4 (N = 20, μ = 97.3%), 20.4 to 38.9 (N = 20, μ = 29.5%), 106.1 to 127.5 (N = 20, μ = 115.5%), 103.5 to 141.8 (N = 20, μ = 116.6%) and 7.0 to 13.3 (N = 13, μ = 10.1%) percent of the length. Maximum inflation at about

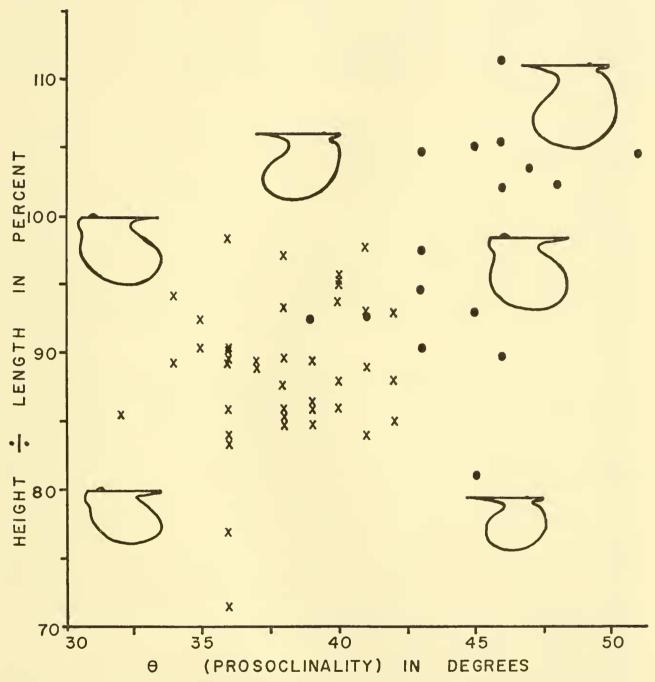


Fig. 13. Scatter diagram of prosoclinality (⊕ in degrees) plotted against form ratio (height expressed as percentage of length), showing large variation of shape of Oxytoma (H.) nebrascana.
X left valves, N = 42
right valves, N = 16

one third of height below dorsal margin, grading posterodorsally into a long narrow pointed posterior ear. Anterior ear not distinct. Byssal ear continuous with dorsal margin, large and prominent; the dorsal margin forms part of the ligament area, the ventral margin projects inward beyond dorsal, separated from anterior margin by a byssal notch of variable width and depth, mostly relatively open, and its inner surface concave. On the outer shell surface a narrow undercut sulcus extends from near the umbo to the notch, and the inner surface of the shell at the end of the notch is thickened (Pl. 14, fig. 5). Umbone insignificant, barely projects above dorsal margin. Prodissoconch and first 1 to 3 mm smooth, remainder of surface is marked by a microscopic, rectangular, reticulate pattern of fine concentric and radial raised lines, sometimes slightly wavy, and of irregular insertion. Ventral margin of reflexed portion of outer shell layer radially plicate to fit into plicae of left valve. A row of irregular small plates or knobs is developed on ventral part of the outer surface of the byssal ear and sometimes on the surface below the byssal notch (Pl. 14, fig. 13).

Posterior to the umbone the dorsal margin of each valve is convex and forms a narrow tube which continues to the end of the posterior ear. This tube is smooth except for faint cross lirae due to growth striae (Pl. 14, fig. 6).

Ligament area extends the length of the dorsal margin of each valve, tapers rapidly posteriorly, widest anterior to umbones, marked by fine longitudinal striae. Area on the left valve inclined ventrally at about 45 to 55 degrees to the commissural plane, that on the right valve subhorizontal although it becomes more steeply inclined on anterior half of byssal ear and inclined at 45 to 55 degrees along the posterior half of dorsal margin. Area with a sharply delimited shallow triangular ligament pit extending from just anterior of the umbones posteriorly for 2 to 4 mm on moderate-size specimens. Anterior margin of pit slightly undercut, initially directed anteriorly and then reflexed to continue posteriorly with increasing growth. The floor of the ligament pit is longitudinally striated.

Monomyarian (but see discussion, p. 85), posterior adductor insertion area large, situated in dorsal third of height just posterior to middle of shell. Left valve insertion generally kidney-shaped (Pl. 14, fig. 10), sometimes elliptical or attentuated ventrally, and slightly larger than the subcircular adductor of the right valve. A deeply impressed small insertion area, about twice as large as the pallial line and other insertions, is situated in umbone under anterior end of the ligament pit. A pallial line of 11 to 16 discrete, small, oval or linear (coalesced) pits extends in a broad asymmetric arc from the umbonal scar to the posteroventral end of the posterior adductor (Pl. 14, fig. 10). The dorsal and ventral scars are the most definite. Two small insertion areas (? visceral, byssal or pedal insertions), but in one case three, are consistently present below the posterior end of the ligament pit and anterodorsal to the adductor. A narrow, faint, rectangular insertion area (the gill suspensory attachment of Newell, 1937, and Ichikawa, 1958, Pl. 24, figs. 10b, c) is present directly below the posteroventral end of the adductor. On the left valve this may be fused to the posteroventral or anteroventral part of the adductor. A small oval or linear insertion (? a pedal protractor) occurs above or fused to the dorsal extremity of the right valve adductor. Some specimens show traces of two to four very small, indefinite insertions above the large insertion area in the umbone.

Ostracum very thin and fragile, up to 0.4 mm thick for specimens greater than 20 mm long, of two layers. A very thin outer layer of possible prismatic structure on both valves, that on the right valve projecting considerably beyond the inner layer, and an inner concentric cross-lamellar layer four to five times thicker than the outer layer.

Types. Location of Evans and Shumard's original specimens unknown. Type locality: "near" Moreau River, South Dakota. Stratigraphic position: probably from the Fox Hills Formation.

Types held at YPM are: hypotypes YPM 24075–90.

Discussion. Measurements were made as shown on Figure 10. Because of the "convexo-concave" relationship of the two valves the inflation of articulated closed specimens is

difficult to obtain. Measurements of the right valve were made on the outline of the inner shell layer of well-preserved specimens. These are false values as many specimens show that the fragile outer layer of the shell reflexes and extends almost to the ventral margin of the left valve along all but the anterodorsal margin below the byssal notch (Pl. 14, fig. 2). In one example (YPM 24080) the inner shell layer extends slightly beyond the point of reflexion. That the reflexion is due to normal growth and not to later compaction is shown by the consistency and regularity of the reflexion, the lack of fracture patterns on specimens (Pl. 14, fig. 2), and the fact that when specimens are crushed the inflated dorsal part is also damaged. Many recent pterioids, i.e. Pteria and Pinctada, have a smaller right valve with a marginal band of the outer shell layer which may be reflexed, but the writer knows of no species with such a marked discrepancy in the size of the convex parts of the valves or such a strong and sharp reflexion. A comparable degree of bending is shown by some extinct strophonemoid and productoid brachiopods. The manner of growth of the right valve of nebrascana is problematical, but the linear increase of the height to length ratio suggests that movement of the reflexion line may be facilitated by the thinness and pliability of the outer shell layer.

The measurements of the right valve were presented above because steinkerns and the outline of the inner shell layer are most easily obtained and are normally the only types of specimens in poorly preserved samples, and also because the left valve sometimes breaks off at the inflexion line and results in apparent equivalve specimens. These could easily cause systematic confusion if found in the geological record. For reference, the relative size of the dimensions of the right valve, as measured from the outline of the inner shell layer, compared to those of the left valve are presented here. Length, height and oblique length of the right valve, respectively, 54.6 to 71.4 ($\mu = 62.3\%$), 58.1 to 66.4 ($\mu = 62.3\%$) and 56.6 to 74.5 ($\mu = 63.7\%$) percent of the comparable left valve measurements for five articulated specimens. The length of the hinge line of both valves on articulated but slightly displaced specimens is about equal, but the umbone of the right valve and ligament pit seem to be situated very slightly posterior to those of the left valve. This is also suggested by the range and mean measurements for the anterior length of the right valve, although a bias could have been introduced if the right valve byssal ear had a flange of inner shell, as on some recent Pteria specimens, or if the ear did not extend to the anterior extremity of the dorsal margin of the left valve.

Qualitative observations on an inadequate number of well-preserved specimens suggest that small specimens are less prosocline than large specimens. Voigt (1954) noted a similar growth trend for O. (Hypoxytoma) danica Ravn. The byssal ear of the right valve fits close against the internal surface of the anterior ear of the left valve which sometimes (YPM 24081; Pl. 14, fig. 12) has thickenings outlining the shape of the byssal ear. The muscle insertion pattern of the right valve is similar to that of O. danica (see Ichikawa, 1958, Pl. 24, figs. 10a, b). The muscle insertion in the anterior part of the umbone is three to four times larger than other possible pedal or byssal insertions, and it is also relatively much larger than the comparable insertion area of living species of Pteria and Pinctada. By analogy to living pterioids, which lack an anterior adductor muscle, although very young pectinids and other monomyarian species possess for a short time a functional anterior adductor muscle (Newell, 1937, p. 22), this large insertion area probably represents a pedal retractor insertion (Pelseneer, 1911). The size and depth of impression of the insertion implies the presence of a relatively large and active foot. Yet as most living pterioids have a relatively small foot (Pelseneer, 1911), it may instead be correlated with a large byssus. The two small impressions below the posterior end of the ligament pit may represent byssal muscle attachments.

The structure of the outer shell layer is uncertain and requires study by thin sections. A fine polygonal pattern visible on the outer surface of both valves suggests a prismatic structure as recorded for the right valve of Oxytoma species by Ichikawa (1958). Ichikawa thought that the entire thickness of the shell of the left valve of his specimens had a cross-lamellar structure.

MATERIAL. About 8500 specimens as individuals and in selected blocks and concretions.

Occurrence. Oxytoma nebrascana occurs in all major assemblage zones of the Trail City and Timber Lake members, but it is common only in the Protocardia-Oxytoma Assemblage Zone of the Trail City Member in which it occurs as a dominant, or as a codominant with Protocardia or Discoscaphites in most assemblages. In other assemblage zones it mostly occurs as scattered specimens, although almost every one, especially those of the Trail City Member exclusive of the Lower nicolleti Assemblage Zone, has one or a few assemblages where Oxytoma is a codominant. Notable cases are assemblages in the Limopsis-Pseudoptera Assemblage Zone, where is it a codominant with Limopsis (Al141) or Pseudoptera (Al170), and in assemblage zones in the Timber Lake Member where it is a codominant with Protocardia and Phelopteria.

Articulated valves are dominant in concretions in the assemblage zones of the Trail City Member, although rare concretions in the Lower nicolleti Assemblage Zone contain single valves, often as a concentration of left or right valves. Single valves are more common, but still subordinate, in the Timber Lake Member, especially in the Tancredia-Ophiomorpha Biofacies, and reflect the higher energy environment. Disarticulated left and right valves, if present, occur in about equal numbers or may be concentrated in different parts of one concretion. Slight displacement and gaping of the two valves is common in many assemblages and reflects the slight transportation and burial sometime after death of the organism. In spite of extreme fragility of the valves breakage is minimal. Much of the incompleteness of the ears and ventral margin is due to extraction. Some of the damage to the ventral margin of valves was perhaps done during the life of the individual, as comparable damage is frequently reported for recent pterioids. Once again breakage is more common in the Timber Lake Member.

Oxytoma nebrascana also shows a restriction of a limited range of size classes to individual concretions, bimodal occurrences, and clustering in a concretion. This is dis-

cussed in the paleozoological text.

The species is frequently reported from Upper Cretaceous sequences in the Western Interior (Robinson and others, 1959) and south-central Canada (Whiteaves, 1885; Gleddie, 1949).

Comparisons. Hypoxytoma nebrascana is distinctive and unlike any other species of the genus described from the Upper Cretaceous of North America. Four species (Woods, 1905; Cox, 1939; Voigt, 1954; Ichikawa, 1958), tenuicostata (Roemer), Campanian; danica (Ravn), Maestrichtian; seminuda (Dames, 1874), Cenomanian; and pectinata (Sowerby, 1836), Lower Cretaceous, common in the Cretaceous of Europe are very similar to nebrascana in size and shape, and in number and form of the costae. By his use of "Avicula nebrascana Evans & Shumard, 1857 (? = Avicula tenuicostata Roemer)", Ichikawa suggests that these two species may be conspecific. The five species are usually separated by differences in size, shape, number of radial costae and the point of appearance of costae. Hypoxytoma danica appears to be distinguished from the other species by its prominent smooth umbones and the late development of costae (at 4 to 11 mm from the umbonal tip; Voigt, 1954). Hypoxytoma pectinata appears to have a height to length ratio greater than that of the other species and to have fewer and stronger primary ribs; tenuicostata differs, on the basis of Woods' figures, from nebrascana by its generally longer posterior ear, which has more numerous radial costae, especially near the dorsal margin, and by the lack of radial lines on the right valve (Woods, 1905, p. 62). The ornamentation of seminuda from the Cenomanion of England is variable. Cox (1939, p. 18) describes specimens on which the costation appears near the tip of the umbone and which are "not distinguishable from Oxytoma tenuicostata", and others which have a smooth umbonal region of up to 8 mm. These appear indistinguishable from danica. The recently proposed O. (H.) danica volgensis Paramonova (1964), Upper Maestrichtian of the Russian platform, has only 20 to 62 radial costae at the ventral margin of the left valve compared to 55 to 100 on O. danica danica, and it may be a distinct species.

The point of appearance of costation may not be of value for separating the species. The same may be true for the apparent smoothness of right valves as the very

thin outer shell layer of nebrascana is easily lost, and also for the shape of the posterior ear because this varies considerably for nebrascana and depends to a large extent on the preservation and distribution of the outer shell layer. A detailed study of large collections is required to determine whether the differences are consistent geographically and stratigraphically, and are of species rank. The differences may then prove to be of stratigraphic importance (Cox, 1939; Voigt, 1954) or may be geographic and/or phenotypic and reflect environmental factors.

SYNCYCLONEMA

Author. Meek, 1864a, p. 31.

Type Species. By original designation, *Pecten rigida* Hall & Meek (1856, p. 381, Pl. 1, figs. 4a-c; *non* Sowerby, 1818, p. 5, Pl. 205, fig. 8 = *Pecten hallii* Gabb, 1861, p. 214), Upper Cretaceous (Maestrichtian), Western Interior, U.S.A.

Discussion. Speden (1967) has fully discussed the status and generic relationships of Syncyclonema. He showed it to be a valid genus belonging the the Pectinidae and to resemble closely Eburneopecten Conrad (1865; Stenzel and others, 1957) in external morphology. The chlamyiid shape, deep byssal notch and internal morphology exclude it from the Entoliidae Korobkov (1960; Newell, 1965). Syncyclonema should not be synonymized with or compared to Entolium Meek (1865).

Syncyclonema halli (Gabb) (Plate 17, figs. 12–17; Plate 18, figs. 1–8)

Pecten rigida Hall & Meek, 1856, p. 381, Pl. 1, figs. 4a-c (non Sowerby, 1818, p. 5, Pl. 205, fig. 8). Pecten hallii Gabb, 1861, p. 214. (Nomen novum for rigida Hall & Meek).

Sincyclonema rigida (Hall & Meek). Meek, 1864a, p. 7.

Syncyclonema rigida (Hall & Meek). Meek, 1864a, p. 31. Meek, 1876, p. 27, Pl. 16, figs. 5a,b. Whitfield, 1880, p. 383, Pl. 7, fig. 1.

Syncyclonema halli (Gabb). Speden, 1967, p. 10, Pl. 1, figs. 1-9; Pl. 2, figs. 1-5; Pl. 3, figs. 1, 2, 4-6.

Types. The following are held at YPM: hypotypes YPM 24112-29.

Discussion. A full description and discussion of S. halli has been given by Speden (1967) and is not repeated here.

MATERIAL. 117 specimens, including eight articulated or displaced bivalves.

Occurrence. Syncyclonema halli is essentially restricted to the Timber Lake Member (92.2%), mainly to the Cucullaea Assemblage Zone, and its relative rarity is indicated by the small number collected. In the five concretions with more than five specimens the valves occurred in a small patch. Twenty-three valves (19.7%) were collected at Loc. 288, Solen, North Dakota, where the species is significantly more common than anywhere in the type area of the Fox Hills Formation.

ANOMIACEA

ANOMIA

Author. Linnaeus, 1758, p. 700.

Type Species. By subsequent designation of Schmidt (1818, p. 71, 177), A. ephippium Linnaeus (1758, p. 701), Recent, Europe.

Anomia gryphorhyncha Meek (Plate 18, figs. 9-17, 22)

Anomia? gryphorhynchus Meek, 1872, p. 375-376.

A. (Placunopsis?) gryphorhynchus Meek, Meek, 1873, p. 509-511.

A. micronema Meek, 1875, p. 43. White, 1879a, p. 165, 190, 208, 211, 215, 217. White, 1883a, p. 97-98, Pl. 3. White, 1883c, p. 57, Pl. 25, figs. 2a-c. White, 1883d, p. 422, Pl. 12, figs. 6-11. Whiteaves, 1885, p. 64.

A. gryphorhynchus Meek. White, 1879a, p. 166, 208, 215, 217. White, 1883c, p. 57, Pl. 25, figs. la-c.

White, 1883d, p. 422, Pl. 12, figs. 12–15.

Description. Length of left valve 2.3 to 26.2 mm, subequivalve, inequilateral to equilateral. Right valve known from one specimen, flat, with faint, irregular concentric growth

depressions, the dorsal part not exposed.

Left valve flat, sometimes with ventral margin reflexed, to strongly convex, orbicular, oval, subquadrangular or subtrigonal. Umbone of small specimens on or projecting above dorsal margin, weakly to strongly incurved and giving a gryphaeoid appearance, those on large specimens inconspicuous, at 2.2 to 7.2 percent of height below dorsal margin. Dorsal or posterodorsal margin sometimes straight, thickened. Height and inflation, respectively, 75.1 to 130.2 (N = 35, $\mu = 102.5\%$) and 2.6 to 43.4 (N = 34, $\mu = 18.3\%$) percent of length. First 1 to 2 mm of shell smooth, main disc with 70 to 130 primary radial costae (mostly 7 to 9 per mm at 7 to 10 mm height), and rare intercalated secondary costae. Costae round-topped, narrow, interspaces two to three times wider and flat-floored, often displaced at growth depressions. Growth lamellae present on wellpreserved shell, the lamellae project as flanges and tend to elongate at costae on one specimen (YPM 24102; Pl. 18, fig. 13). A small specimen has weak, broad radial plicae (YPM 24100; Pl. 18, fig. 15).

Ligament internal, borne on a small elongate, concave resilifer sited in umbonal cavity, its dorsal margin with a V-shaped depression. Left valve with four muscle insertion areas; a small oval anterior byssal retractor under anterior end of resilifer, and on the white calcitic plug an L-pattern of three large oval partly confluent insertions, a large byssus retractor, a posterior adductor about half the size, sometimes elongated, fused to ventral margin of retractor, and a slightly smaller posterior byssal retractor fused to posterior margin of adductor, or discrete. Central insertion area on small specimens a narrow band with ventral part reflexed posterodorsally, weakly differentiated into the three parts.

Ostracum up to 0.7 mm thick, of one to three layers. Umbones and outer margins of shell formed of outer subnacreous layer composed of subparallel lamellae. The center of disc with an inner plug of white calcite that appears homogeneous but shows traces of laminae in parts, and shell under muscle scars of three layers with, in addition to above two, an inner prismatic layer that comprises about half the thickness of shell.

Types. No lectotypes have been designated for A. gryphorhynchus Meek and A. micronema Meek. No lectotypes are selected here as the writer believes they should be chosen as part of a revision of the North American Upper Cretaceous species.

Types held at YPM are: hypotypes YPM 24097-24104.

MATERIAL. 65 large specimens from the *Crassostrea subtrigonalis* shellbeds of the Colgate lithofacies, and 35 small specimens from the Trail City Member, of which 31 come from the Lower *nicolleti* Assemblage Zone.

Discussion and Occurrence. Except for one small articulated specimen from Loc. 44, only left valves were found. In the Colgate oyster banks specimens are rare, occur in small patches or as discrete individuals and are worn to varying degrees. In the Trail City Member assemblage zones the species occurs as less than three scattered valves per concretion.

The length of specimens collected from the Trail City Member and Colgate lithofacies are less than 11.4 mm and greater than 16.2 mm, respectively. This gap in sizes, the virtual restriction of specimens to the Lower nicolleti Assemblage Zone in the Trail City Member, and the dominance of convex forms in the Colgate lithofacies suggested that two species may be present, the small convex forms resembling A. gryphorhyncha Meek and the larger flatter forms, A. micronema Meek. As both flat and strongly convex forms are present in collections from one concretion in the Lower nicolleti Assemblage Zone and from the same patch in an oyster bed, as samples in both size ranges have the same shapes represented, and as large and small specimens have the same number of costae (7 to 9 per mm at 7 to 10 mm height), the environmental separation does not seem an adequate basis for species distinction, particularly in view of the known variation of recent species (Dall, 1898; Lamy, 1940; Merrill, 1962). The possibility of wide dispersal of Anomia species is provided by a pelagic larval stage that inhabits surface waters (Merrill, 1962). Further support for the identity of the two stratigraphically separated size groups is the similar range of measurements and mean values. The height to length percentages of the small specimens from the Trail City Member and the large from the Colgate lithofacies are, respectively, 80.5 to 128.9 (N = 18, μ = 101.7%) and 75.1 to 130.2 (N = 17, μ = 103.4%), and the width to length are respectively 2.6 to 33.3 (N = 18, $\mu=18.0\%$) and 5.9 to 43.4 (N = 16, $\mu=18.8\%$) percent. Meek himself (1873, p. 510) recorded that flat specimens occurred with the typical convex specimens of gryphorhyncha at the type locality. The musculation pattern of both forms is similar and matches that shown for a specimen of gryphorhyncha illustrated by White (1883d, Pl. 12, fig. 15) who noted that micronema and gryphorhyncha sometimes occurred together in the same layer.

The small gryphaeoid specimens tend to resemble comparable-size specimens of *Crenella* but the subnacreous shell structure and the internal resilifer (Pl. 18, fig. 14) in the umbone places then in *Anomia*.

Comparisons. The known great variation of recent species of Anomia suggests that Upper Cretaceous species could be equally variable morphologically. If this proves to be the case, many of the species recorded from the Upper Cretaceous strata of the Western Interior are probably synonymous. A comprehensive review of the species is required before a detailed synonymy can be prepared. White (1883d, Pl. 12, figs. 15a, b) noted that his propatoris closely resembled gryphorhyncha and he considered it to be intimately related to micronema. His figured specimens, and those of Stanton (1893, Pl. 8, fig. 10) closely resemble smaller specimens from the type Fox Hills, and the species is probably conspecific. Anomia subquadrata Stanton (1893, Pl. 8, figs. 8, 9; USNM 22864) has a similar shape, and it may be conspecific with gryphorhyncha. Numerous species with fine radial costae have been named from Gulf and Atlantic Coastal Plain localities. Some specimens, notably of ponticulana Stephenson (1952), olmstedi Stephenson (1923), lintea Conrad and argentaria Morton, closely resemble gryphorhyncha in shape and ornamentation.

The original collection (USNM 7828), from Point of Rocks, Wyoming studied by Meek contains strongly convex, gryphaeoid and flat specimens of variable shape some of which match gryphorhyncha and others micronema. These two species are undoubtedly conspecific.

OSTREACEA

OSTREA

AUTHOR. Linnaeus, 1758, p. 645, 696.

Type Species. By Linnaean tautonymy (ICZN Opinion 94), Ostrea edulis Linnaeus (1758, p. 218), Recent, European coasts from Norway to the Mediterranean.

Discussion. The morphological variation of oysters within one environment, much of which is due to competition for space during growth, and in different environments is well known (Gunter, 1950; Thomson, 1954). Some zoologists (Nelson, 1938, p. 56; Ranson, 1942) have noted that it is difficult to separate genera and species on the basis of external shell characters alone, particularly if the specimen or population has undergone extreme growth distortion. Recent oysters are classed in three genera, Ostrea, Crassostrea and Pycnodonte, by morphological, anatomical and physiological features (Gunter, 1950; Thomson, 1954), and by the characters of the prodissoconch (Ranson, 1948, 1960). Pycnodonte is distinctive in many features and is not considered further here. In some cases the classification of fossil specimens into Ostrea or Crassostrea is difficult. Features of paleontological value are the general shape, position and shape of the adductor muscle, the convexity of the lower and upper valves, and the presence and size of the umbonal cavity, all of which, especially the second, are related to the presence or absence of the promyal chamber (Nelson, 1938). The shell of Ostrea tends to be oval to subquadrangular and flattish, the adductor muscle is subcentral and generally not colored, and an umbonal cavity is absent or poorly developed on the left (lower or attached) valve. The shell of Crassostrea is elongated, the left valve is convex, and if it is flat the right is convex, the adductor muscle is displaced posteriorly toward the posteroventral margin and it is usually colored, and an umbonal cavity is generally developed on the left valve and sometimes also on the right valve. Exceptions abound within species in each genus. For example, elongated specimens of O. equestris Say, which has no promyal chamber (Nelson, 1938, p. 15), have the adductor muscle in a position typical of Crassostrea, frequently very close to the posterodorsal margin, and some specimens tend to be elongated as for Crassostrea. Some specimens of equestris have an umbonal cavity but this is not deep and was not seen on right valves. Vice versa, numerous specimens of C. virginica lack an umbonal cavity on the left valve. It is the general possession of the complex of the morphological features listed above and their relatively consistent presence that is characteristic at the generic level.

One of the two oysters common in the Fox Hills Formation is an undoubted Crassostrea. It closely resembles virginica and follows the same mode of life. The other species, translucida (Meek & Hayden), is restricted to marine environments and is tentatively classed in Ostrea. Its general flat, curved cupped shape does not resemble typical Ostrea but more closely approaches Crassostrea. The adductor scar is situated close to the posterodorsal margin and is not central as in typical Ostrea or ventral as for typical Crassostrea. Most specimens of translucida have a finely corrugated posterodorsal margin, many have a weakly plicated ventral margin, while a few have a strongly corrugated ventral margin and so resemble Lopha. The status of Lopha is uncertain. Some authors (Cox, 1952) accept it as a valid genus, maintaining that there is a distinct stock of plicated oysters ranging from the Jurassic to the present day. Most biologists do not accept the

taxon (Yonge, 1960). Ranson (1942), on the basis of prodissoconch studies, places crista-galli, the type species of Lopha, in Ostrea, and Thomson (1954), after a study of the great variability of Australian specimens, synonymizes crista-galli under Ostrea folium Linnaeus. O. translucida resembles the Upper Cretaceous O. ungulata (Schlotheim), the type of Agerostrea Vialov (1936), and O. lunata Nilsson, and could be classed in Agerostrea.

Population and phylogenetic studies are required to clarify the status of many fossil form genera. Until shown otherwise the gross morphology and environmental occur-

rence of translucida favors classification in Ostrea.

Ostrea translucida Meek & Hayden (Plate 18, figs. 18–21; Plate 19, figs. 1–22)

Ostrea larva Hall & Meek, 1856, p. 406 (non O. larva Lamarck, 1819, p. 216). Meek & Hayden, 1856c, p. 286.

Ostrea translucida Meek & Hayden, 1857, p. 147. Meek & Hayden, 1860b, p. 429. Meek, 1864a, p. 6. Ostrea pellucida Meek (non Defrance, 1821, p. 26), 1876, p. 15, Pl. 28, figs. 4a,b. White, 1884, p. 299, Pl. 50, figs. 6, 7. Warren, 1934, p. 85.

Ostrea (Gryphaeostrea) subalata Meek, 1876, p. 15, Pl. 28, fig. 5.

DESCRIPTION. Small, specimens 1.0 to 38.7 mm long, equivalve or slightly inequivalve, inequilateral. Left (attached) valve weakly to strongly convex, maximum inflation normally in dorsal third, with an umbonal cavity of variable prominence, and right valve mostly flat or weakly convex, sometimes moderately to strongly convex, when it has an umbonal cavity. Shape extremely variable, typically elongated subquadrangular with the ventral end curving posterodorsally, sometimes straight rectangular, trigonal, or oval (Pl. 19). Width of shell perpendicular to growth axis extremely variable. Umbonal margin sometimes straight, the posterodorsal side commonly and the anterodorsal side rarely auriculate. Height and width, respectively, 57.4 to 161.5 (N = 37, μ = 112.6%) and 14.1 to 36.8 (N = 36, μ = 24.5%) percent of length for left valves, and 72.6 to 154.5 (N = 47, $\mu = 112.6\%$) and concave or 5.8 to 34.6 (N = 44, $\mu = 14.4\%$) percent of length for right valves. Area of attachment on left valve large to minute. Umbones terminal, straight to twisted, small to large, that on left valve generally more projecting. Ligament area triangular, trapezoidal, or a narrow band along the umbonal margin, larger on the left valve; length and height of ligament area, respectively, 16.5 to 40.3 (N = 31, μ = 25.9%) and 6.0 to 20.3 (N = 31, μ = 11.0%) percent of the length and height of left valve, and 15.3 to 39.7 (N = 39, μ = 24.7%) and 4.6 to 12.5 (N = 39, μ = 8.2%) percent of the length and height of the right valve. The height of the ligament area, respectively, 24.1 to 86.2 (N = 31, μ = 48.7%) and 13.0 to 70.2 (N = 39, μ = 39.2%) percent of the length of the ligament area for the left and right valves. Ligament area of left valve with a triangular pit of variable prominence for reception of inner ligament layer (Trueman, 1951); right valve with a matching indefinite shallow depression or raised area, or flat, and with an inward-protruding ventral margin.

Outer surface with growth lamellae overlapping and often strongly imbricate marginally and ventrally, irregular growth depressions, and with a few faint radial costae on rare specimens. Ventral and anterior margins with nought to five, commonly none and rarely more than three, broad plicae of irregular strength (Pl. 19, fig. 19). Posterodorsal margin with nought to 10 short round-topped, semiregular plicae, often with strongly imbricate growth lamellae. Internal margin of right valve with a row of nought to 24, faint to strong, nodose hollow denticles along posterodorsal margin and less commonly nought to 15 on the anterodorsal margin. Denticles generally few, restricted to posterodorsal margin between ligament and appearance of plicae, strongest on those specimens

with a wing (Pl. 19, figs. 6, 14). Left valve with matching sockets.

Monomyarian, adductor insertion scar large, moderately impressed, subquadrangular, the margin toward the ligament concave, situated close to posterodorsal margin with the base of the insertion at 31.4 to 51.1 (N = 53, μ = 43%) percent of the "height" below the dorsal margin of the ligament. A small oval insertion (branchial retractor of Pelseneer, 1911, p. 27; Quenstedt's muscle of Stenzel, 1963, fig. 1) of variable prominence is situated immediately below the ventral margin of the ligament anterior to its mid-length.

Main disc of ostracum up to 0.8 mm thick, consisting of two layers, a very thin outer prismatic layer and a thick inner subnacreous lamellar layer (Tsujii and others, 1958). Outer layer normally worn off.

Types, Lectotype of O. translucida Meek & Hayden, USNM 330, by subsequent designation of Meek (1876, in caption to Pl. 28, fig. 4a), a left valve, L=19.1, H=24.8, $\frac{1}{2}$ W = 7.8 mm. Type locality: Long Lake, North Dakota. Stratigraphic position: Fox Hills Formation, probably Timber Lake Member. Lectotype of Ostrea subalata, by subsequent designation of Meek (1876, in caption to Pl. 28, fig. 5), a two-valved shell, L=18.6, H=27.1, $\frac{1}{2}$ W = 18.3 mm. Type locality: Moreau River, South Dakota. Stratigraphic position: Fox Hills Formation. The associated fossils and lithology indicate derivation from the Timber Lake Member.

Types held at YPM are: hypotypes YPM 24386-94, 24722-37.

Discussion. The marked variation in all morphological features is due in part to the space available for growth and the size of the attachment area. If the attachment area occupies more than half the area of the left valve it may be flat, and the right valve is then strongly inflated and possesses a deep umbonal cavity. As is the case for many oysters, the right valve of *translucida* tends to be thinner than the left (Thomson, 1954). Most specimens attached to shells, mostly of *Phelopteria* and secondarily of *Ostrea*, and to a small extent to plant fragments.

At Locality 83, Tancredia-Ophiomorpha Biofacies, small shells (less than 3 mm length) are attached to the exterior of 46 (46% of total) valves, and to the exterior and interior of three valves. Left valves (61%) are more frequently encrusted than right valves. When an articulated specimen has epizoans they are always more numerous on the left and are frequently concentrated around the ventral margin. Those right valves that have attached specimens occur in clumps, and during life were probably shaded or facing downward to varying degrees. The dispersal of "spat" suggests that the larvae were in part negatively phototrophic as are those of modern oysters (Nelson, 1921; Hopkins, 1935). The attraction for an undersurface is partly due to protection from siltation (Korringa, 1940).

MATERIAL. About 1090 specimens as individuals and in selected blocks and concretions.

Occurrence. Common in the marine phase of the Timber Lake Member and the Tancredia-Ophiomorpha Biofacies. Very rare in the other members. O. translucida does not form reefs. It occurs only as single specimens, in clumps (Locs. 33, 73, 83), or as a dominant or codominant in a few assemblages, mainly Ostrea, Ostrea-Phelopteria, Ostrea-Tellinimera, and Ostrea-Cucullaea. Most of the patches, as at Loc. 83, have grown on a base of shell fragments. Where the species is a dominant most specimens are attached to shells, mainly Phelopteria, or rarely to wood, mostly as one specimen per shell or in small groups of less than 10. Nearly all the associations dominated by Ostrea show evidence of minimal transportation and this and the frequent concentration of the species in patches within concretions indicate derivation from clusters. No case was found where the oysters formed a cap to a concretion, so indicating settlement in place. About half of the Phelopteria specimens forming the attachment are articulated and may have been alive during part at least of the oyster's life. This is supported by the dominance of articulated specimens of translucida in most assemblages and by the lack of spat encrustations on species other than Ostrea and on the inside of valves (see above). Encrustation is uncommon except in the Tancredia-Ophiomorpha Biofacies. This suggests relatively rapid burial or environmental conditions unsuitable for many spatfalls.

The high percentage of single valves in the collection from Loc. 83 is due to intensive collection from rainwash concentrates, for at this locality most specimens occur in small patches attached to shells or wood.

Comparisons. Some nomenclatural confusion was caused by Meek's (1876, p. 15; see also White, 1884, p. 299) forgetting his earlier name (translucida) for specimens from the same locality, Long Lake and Moreau River, and his proposal of the preoccupied name pellucida. Meek's description of translucida is applicable to undoubtedly conspecific material from the type area of the Fox Hills, and even though no illustration accompanied his description, the name is available under the International Code of Zoological Nomenclature (Stoll and others, 1964). Meek (1876) described a second species, O. (Gryphaeostrea) subalata, from Moreau River. The figured specimen, the right valve of an articulated specimen, has the same general shape as translucida and unquestion-

ably is conspecific, yet it is slightly more alate than any collected by the writer.

The specific relations of translucida and its validity as a species are uncertain. Individual specimens from Loc. 83 are indistinguishable from figured specimens of O. (Alectryonia) larva Lamarck (White, 1884, Pl. 42, figs. 4, 5, 6), O. larva var. nasuta Morton (Whitfield, 1885, Pl. 3, figs. 3, 4), O. mesenterica Morton (Weller, 1907, Pl. 43, figs. 10-14), O. larva subsp. mesenterica Morton (Gardner, 1916, Pl. 22, fig. 5), and O. mesenterica Morton? (Stephenson, 1941, Pl. 16, figs. 7, 9). Specimens are also indistinguishable from some included in the European O. larva, O. lunata Nilsson, and O. ungulata (Schlotheim), as is indicated by Woods' (1913, p. 393) inclusion of the O. (Alectryonia) larva of White (1884), O. l. var. nasuta of Whitfield (1885), and nasuta and mesenterica of Weller (1907) in his O. lunata Nilsson. Ostrea translucida closely resembles lunata as interpreted by Woods but most specimens do not have such a lunate shape. Detailed population studies are required to solve the species relationships of the similar species from the Upper Cretaceous of Western Europe, the Atlantic and Gulf Coastal Plains, and the Western Interior of the United States. As these have not been done and as the "typical" shape of translucida is less alate, is not as regularly plicate, and lacks the straight dorsal margin of "typical" falcata (? = larva) of the Atlantic Coastal Plains sequences, translucida is here retained as a valid species.

CRASSOSTREA

AUTHOR. Sacco, 1897, p. 15.

Type Species. By original designation, Ostrea virginica Gmelin (1791, p. 3336), Recent, along the east coast of North America.

Discussion. Crassostrea subtrigonalis closely resembles virginica and differs only in possessing strong denticles around the dorsal margins of the valves. Some juveniles of virginica (YPM 7056) also have these denticles but they are uncommon and are rarely present on adults. The function of these denticles is unknown, and because of the complex of the other characters they are unlikely to be of major systematic importance.

Sohl and Kauffman (1964), in an important contribution to the study of fossil oysters, have emended the diagnosis of the genus and clarified the terminology of morpho-

logical features.

Crassostrea subtrigonalis (Evans & Shumard) (Plate 19, figs. 23, 24; Plate 20, figs. 1–11)

Ostrea subtrigonalis Evans & Shumard, 1857, p. 40.

Ostrea glabra Meek & Hayden, 1857, p. 146 (non Ostrea glabra Linnaeus, 1758, p. 698). Meek, 1864a, p. 6.

Ostrea wyomingensis Meek, 1872, p. 375. Meek, 1873, p. 508-509.

Ostrea arcuatilis Meek, 1873, p. 447.

Ostrea insecura White, 1876, p. 112-113.

Ostrea subtrigonalis Evans & Shumard. Meek, 1876, p. 510, Pl. 40, figs. 1a-d. White, 1883d, p. 421, Pl. 12, figs. 2-5; 1884, p. 308, Pl. 60, figs. 1-4, Pl. 61, figs. 1-2. Whiteaves, 1885, p. 5, 30,

56, 83. Warren, 1931, Pl. 3, fig. 4. Fisher and others, 1960, p. 35.

Ostrea glabra Meek & Hayden. Meek, 1876, p. 509, Pl. 40, figs. 2a-d. White, 1879a, p. 167-168, 190, 208, 215-218; 1883d, p. 421, Pls. 9-11, 12, fig. 1; 1884, p. 307, Pls. 58-60, 61, fig. 1. Whiteaves, 1885, p. 5, 56, 64. Williams and Dyer, 1930, p. 43. Warren, 1931, Pl. 3, figs. 3, 12. Fisher and others, 1960, p. 34.

Ostrea arcuatilis Meek. White, 1883d, p. 421, Pl. 10, fig. 5 (as a variety of glabra); 1884, p. 307, Pl.

59, fig. 5 (as *glabra*).

Ostrea insecuris White. White, 1883d, p. 421, Pl. 10, figs. 3, 4 (as a variety of glabra); 1884, p. 307, Pl. 59, figs. 3, 4 (as glabra).

Ostrea wyomingensis Meek. White, 1883d, p. 421, Pl. 11, figs. 1-4 (as a variety of glabra); 1884, p. 307, Pl. 60, figs. 1-4 (as glabra).

Ostrea glabra arcuatilis Meek. Schuchert, 1905, p. 469.

Ostrea glabra wyomingensis Meek. Schuchert, 1905, p. 469.

Crassostrea glabra (Meek & Hayden). Cvancara, 1966, p. 320, Pl. 4, figs. 3-6; Pl. 5, figs. 10-12.

DESCRIPTION. Grows to large size, specimens 4.8 to 77.9 mm long and 6.4 to 102.2 mm high, shell thick to massive on large specimens, inequivalve, inequilateral. Left valve cup-shaped, with maximum inflation in dorsal third, but sometimes ventral or along anterior margin, rarely flat. Umbonal cavity of variable prominence, sometimes absent. Right valve not as thick, flat, rarely weakly convex or concave with the ventral margin reflexed outward, without an umbonal cavity. Shape extremely variable, typically straight and elongated-rectangular, some specimens subquadrangular, subtrigonal, or with the ventral extremity reflexed posterodorsally (generally) or anterodorsally (Pl. 20). Height and width, respectively, 88.3 to 231.2 (N = 57, μ = 154%) and 12.6 to 49.3 (N = 49, $\mu = 30.7\%$) percent of length of left valve, and 120.7 to 215.1 (N = 20, $\mu = 163.3\%$), and concave or 8.8 to 24.5 (N \pm 20, μ = 15.3%) percent of length of right valves. Area of attachment on left valve large to small. Umbones terminal, very variable in shape and prominence, straight or twisted clockwise or anticlockwise. Ligament area also of variable shape, trigonal and projecting, or a narrow band along margin, that on the right valve smaller. Length and height of ligament area, respectively, 19.2 to 57.7 (N = 56, μ = 33.7%) and 7.0 to 25.1 (N = 56, μ = 15.1%) percent of length and height for left valves, and 21.3 to 44.5 (N = 19, μ = 33.6%) and 6.5 to 15.6 (N = 19, μ = 10.9%) percent of length and height for right valves. Height of ligament area for left and right valves, respectively, 27.6 to 154.3 (N = 56, $\mu = 70.6\%$) and 29.5 to 87.1 (N = 19, $\mu = 52.2\%$) of length of ligament area. Ligament area of left valve with a triangular pit, usually strongly impressed, for reception of inner layer of ligament, and right valve with a matching protuberance that projects inward and ventrally to form a lip.

Outer surface with growth lamellae, best developed on right valves, and growth depressions, smooth, or with fine or coarse radial costae, 20 to 61 in number, generally faint or worn off and present only on the juvenile stages of left valves. On either side of the ligament the inner dorsal margins of the right valve have a row of nought to 20, mostly less than 10, and frequently absent on the anterodorsal margin, hollow denticles of variable prominence. Dorsal margin of left valve with matching sockets which are often situated on the side of a groove into which fits the dorsal margin of the right valve (Pl.

20, fig. 6).

Monomyarian, adductor insertion area large, moderately impressed, subelliptical, subquadrangular or comma-shaped, the margin toward the ligament weakly to strongly concave, situated very close to the posterior margin with its base at 19.1 to 43.8 (N = 64, $\mu = 33.4\%$) percent of the height. A small oval insertion (gill retractor; Ryder, 1884, Pl. 73, fig. 1) is situated below ligament anterior to its mid-length.

Main disc of ostracum up to 5 mm thick, sometimes twice as thick in umbonal region, consisting of two layers, a very thin outer prismatic layer and a thick inner sub-

nacreous lamellar layer. Outer layer normally worn off.

Types. Location of Evans and Shumard's original collection unknown. Type locality: Owl Butte, between Grand and Moreau Rivers, South Dakota. Stratigraphic position: Fox Hills Formation, almost certainly from the Colgate lithofacies. Lectotype of Ostrea glabra Meek & Hayden, USNM 2165, by subsequent designation of Meek (1876, in caption to Pl. 40, fig. 2a), a poorly preserved left valve, L=54.8, H=73.3, $\frac{1}{2}$ W=20.2 mm (Meek, 1876, Pl. 40, figs. 2a,b). Type locality: Mouth of Judith River, Montana. Stratigraphic position: Judith River Formation, Campanian. For data on Ostrea wyomingensis, arcuatilis and insecura, see Schuchert, 1905.

Types held at YPM are: hypotypes YPM 24417-22, 24717-21.

Discussion. The shell form of this species is extremely variable and is in part related to the size of the area of attachment and to the space available for growth. Some specimens resemble the coon oyster shape of some recent virginica. In most cases the denticles are restricted to the juvenile growth stages, being exposed as tubules on the outside dorsal margins of right valves (Pl. 20, fig. 4). This limitation may have some functional significance. Specimens at many localities, especially at Loc. 84, are riddled by borings resembling those made by clioniid sponges in recent oyster shells. The anteroventral margin, adjacent to the inhalant area, of one specimen from Loc. 16 has large borings similar to those made by species of the bristle-worm Polydora. These borings are in a position favored by present-day species (Yonge, 1960, p. 128).

MATERIAL. Approximately 400 specimens, 170 as single valves or articulated specimens, the remainder in selected blocks.

Occurrence. Crassostrea subtrigonalis is restricted to the Colgate lithofacies and to a few localities in the Hell Creek Formation. In both of these units it forms shellbeds which may reach oyster bank size. Banks very commonly cap buttes in the type area of the Fox Hills, as at Locs. 16 and 84, and also in the Hell Creek at Loc. 75. At Loc. 16 the bank is 50 by 30 yards and is about 15 feet thick. Both the shellbeds and banks lack original growth structures, the shells being aligned subparallel to the bedding in most cases. Currents probably have modified the shellbeds and erosion has removed the margins and caps of the bank. Both single valves and articulated specimens are present, the former apparently dominating, with much attachment and encrustation of smaller or later specimens to insides and outsides of valves as occurs in present-day banks. The most common associated pelecypods are species of Corbicula which occur as scattered specimens or in distinct beds intimately associated with subtrigonalis beds.

Crassostrea subtrigonalis has been recorded widely from Upper Cretaceous sequences of the Western Interior (White, 1879a, 1884; Fisher and others, 1960) and Canada (Whiteaves, 1885; Warren, 1931).

Comparisons. The specimens on which Evans and Shumard based their description came from "the vicinity of Owl Butte, between Moreau and Grand Rivers", and were noted as being "very variable". Although the specimens most certainly came from within the type area of the Fox Hills, the exact locality of the butte is unknown. Meek (1876) was the first to illustrate specimens that he ascribed to subtrigonalis, but he was unsure of their specific identity with Evans and Shumard's subtrigonalis. Meek's specimens of subtrigonalis and glabra came from the same locality, the Judith River Beds. Because of intergradational forms, White (1879b, 1883d, 1884) gradually became convinced that wyomingensis, arcuatilis and insecura were conspecific with glabra. He had some reservations about synonymizing subtrigonalis with glabra mainly because (1884, p. 308) his specimens of subtrigonalis seemed to be uniform in size and shape and considerably smaller than those of glabra. Yet, in 1879a (p. 218) he regarded subtrigonalis to be "young examples" of wyomingensis and glabra. Specimens closely resembling, and others that intergrade between, the types or figured specimens of all species listed above have been collected by the writer at localities in the type area of the Fox Hills, and with

perseverance matching specimens could be collected. There is little doubt that the five species are conspecific although data on populations from the type localities are required to prove this conclusively.

Crassostrea glabra Meek & Hayden is a junior primary homonym and must be permanently rejected (ICZN Art. 59a).

CORBICULACEA

CORBICULA

AUTHOR. Megerle von Mühlfeld, 1811, p. 56.

Type Species. By subsequent designation of Gray (1847, p. 184), Tellina fluminalis Müller (1774, p. 205) (= Tellina fluminalis Gmelin, 1791, p. 3242), Recent, eastern Europe and western Russia.

Discussion. Three form groups, here called elliptical, oval, and high-oval, can be recognized in small samples. The high-oval group includes strongly inflated, thick-shelled, globular specimens with prominent incurving opisthogyrous umbones (Pl. 21, fig. 9). These are equivalent to *C. occidentalis* (Meek & Hayden). The elliptical group includes thin- to moderately thick-shelled compressed elliptical specimens whose height is about 60 to 80 percent of length (Pl. 21, figs. 2, 13). These have been named *C. subelliptica* (Meek & Hayden) and *C. subelliptica* var. moreauensis (Meek & Hayden). The elliptical group grades into and is arbitrarily defined by height to length > 80 percent, from compressed or moderately inflated oval individuals which have thick or thin shells, prominent or weak umbones and height of about 80 to 95 percent of length (Pl. 21, figs. 6, 8). Included are forms that could be named nebrascensis (Meek & Hayden) or cytheriformis (Meek & Hayden).

Because of the need for further sampling and biometric study, the Fox Hills specimens are classed in one species and a general description given.

Corbicula sp. A (Plate 21, figs. 1–13)

DESCRIPTION. Specimens in these three groups have an anterior length of about 30 to 50 percent of length, with the high-oval and elliptical tending to have more anteriorly placed umbones and the oval more posterior umbones. Dentition and musculation are identical. Any minor differences are due to shell shape.

Heterodont, three stout lamellar cardinal teeth in each valve, the right valve anterior shorter, more conical and less projecting than the other two, and the posterior of the left valve weaker, fused to nymph. Apex of sockets with short secondary teeth. With growth the spaces between the secondary and cardinal teeth become filled with aragonite (vincula; Casey, 1952). Left valve with one anterior and one posterior long lamellar lateral tooth, the anterior of variable thickness. Right valve with two weakly projecting anterior and posterior round-crested laterals, the dorsal delimited from the shell margin by a narrow shallow groove. Cardinal and lateral teeth and sockets serrated. Nymphs strong, projecting, short or long, 14 to 27 percent of length. Ligament external, sometimes sunken posteriorly.

Muscle insertion areas weakly to strongly impressed, subequal, suboval. Anterior adductor insertion more impressed than posterior, especially along dorsal margin which may have a slight bulge (= pedal retractor). Posterior adductor continuous with a nar-

row pedal retractor scar extending for a short distance under hinge. Anterior pedal insertion elliptical, strongly impressed, separated from adductor. A line of small discrete oval to elongated insertions continues posteriorly under hinge to below posterior cardinal tooth, where there is sometimes a larger insertion area. Pallial sinus small, asymmetric.

Ostracum up to 5 mm thick in umbonal region, of two layers. A thick outer concentric cross-lamellar layer and, below the myostracum and inside pallial line, a complex cross-lamellar layer.

Types. The following are held by YPM: hypotypes YPM 23874, 23878-79, 24395-96, 24398-99, 24401, 24712-14; measured specimens 23872-73, 23875-77, 23880, 24402, 24715.

Discussion. Graphs (Figs. 14, 15) show the gradation of the compressed elliptical form into the oval group of more inflated and higher specimens. The high-oval specimens appear to be distinctly separated by their height to length ratio and to a lesser degree by inflation. The separation between the high-oval and oval groups is probably apparent and due to poor sampling and low numbers of the high-oval specimens. Incomplete specimens suggest that the gap could be filled. Growth lines on well-preserved valves indicate that initially the high-oval and elliptical individuals have somewhat similar height to length ratios but that the height to length percentage increases significantly in the first case and remains about constant in the second (Fig. 15). The measurement data suggest the possibility of two species with the juveniles and extreme individuals being indistinguishable when mixed together or if they lived sympatrically. The geographic occurrence of the specimens is inconclusive. All three form groups occur together in the oyster bed at Dog Butte (Loc. 16). Only high-oval forms were collected at Loc. 97, and elliptical and oval groups at the remaining localities. The three form groups occur together in about equal numbers in the sample from Loc. 16.

Because of poor sampling the relative abundances may not be significant. The sampling and the tendency for some of the elliptical specimens to have an initial increase in height to length ratio (Fig. 15) makes it impossible to decide whether the growth trends are artifacts of phenotypic variation or are due to genetic control. Although the shape of species of *Corbicula* is known to be variable, I could find no example of a species following two growth trends. As the sampling and data are inadequate, the form groups are tentatively placed under *Corbicula* sp. A. Recognition of two species would be a more conservative procedure.

MATERIAL. About 300 specimens.

Occurrence. Restricted to the Colgate lithofacies where it occurs as discrete beds, sometimes closely associated with oyster beds (Loc. 74), and as scattered specimens in oyster beds. Some *Corbicula* beds (Loc. 91) have a high proportion of articulated specimens, others a low number (Loc. 74) and approach a shell-hash. The "species" is present in an estuarine *Crassostrea* bed at Loc. 75, Hell Creek Formation.

LEPTONACEA

SPANIORINUS

Author. Dall, 1900, p. 1123.

Type Species. By original designation, Scintilla cossmanni Dall (1900, p. 1125), Miocene, Virginia.

Discussion. Spaniorinus, originally proposed as a subgenus of Solecardia Conrad (1849),

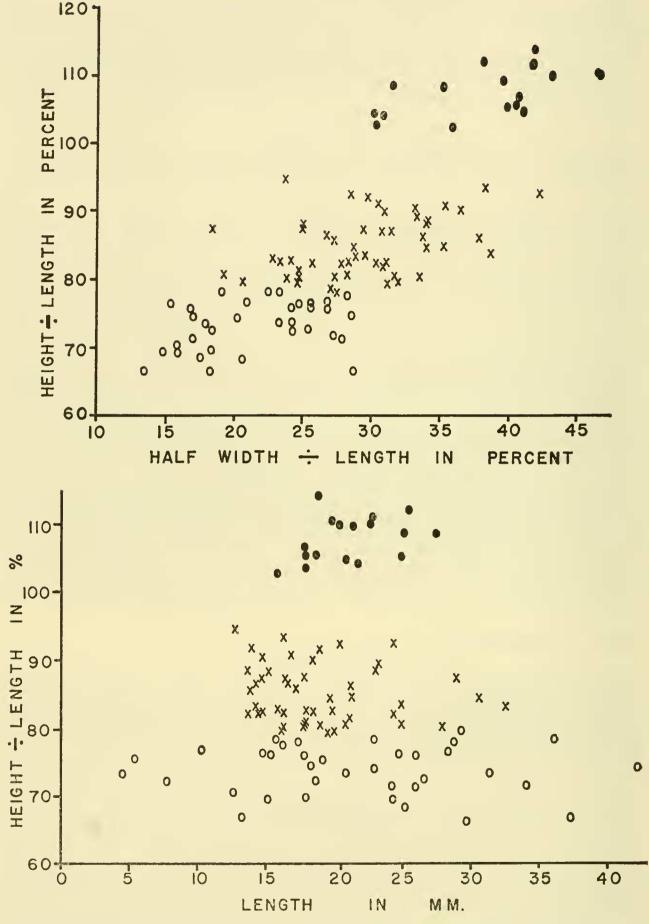


Fig. 14. Corbicula sp. A. Scatter diagram of length plotted against form ratio (height expressed as percentage of length) and form ratio plotted against half width expressed as percentage of length, showing relations of three arbitrarily selected groups. Specimens mainly from Localities 16 and 264. \bullet = high-oval shape, N = 17; x = oval shape, N = 52; o = elliptical shape, N = 36.

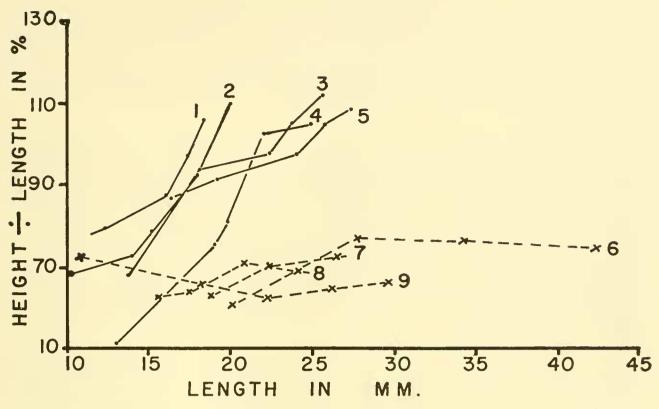


Fig. 15. Corbicula sp. A. Growth trends of selected specimens, based on measurement of growth lines of large elliptical (---) and high-oval (----) specimens.

- 1. YPM 23875, Loc. 16, A256
- 2. YPM 23876, Loc. 16, A256
- 3. YPM 23873, Loc. 16, A256
- 4. YPM 23874, Loc. 16, A256
- 5. YPM 23872, Loc. 97, A950

- 6. YPM 23878, Loc. 264, A299
- 7. YPM 23880, Loc. 264, A299
- 8. YPM 23877, Loc. 16, A256
- 9. YPM 23879, Loc. 264, A299

was raised to generic rank by Cossmann and Peyrot (1911, p. 213). This move is supported by the occurrence of adductor impressions inside the pallial line in *Solecardia*, whereas they are incorporated in the pallial line in *Spaniorinus*. Kautsky (1939) states that the genus ranges from Eocene to Recent. It is most common in lower Tertiary sequences.

Spaniorinus nicolleti sp. n., described below, differs from typical species in several aspects which are not considered of generic rank. Future work may prove them to be of subgeneric value. The shell is thicker, the muscle scars and pallial line are more impressed, the prominent, flat, featureless areas anterior to the cardinal tooth and posterior to the sunken resilifer are not evident on species figured by Cossmann and Peyrot or other workers, the dorsal margin of the right valve tends to overlap and interlock with that of the left valve, and an anterior ridge extends toward the anterior adductor scar from near the umbonal cavity. In spite of careful preparation no small protuberance (4b of Cossmann and Peyrot) was observed fused to the posterodorsal part of the cardinal tooth of the left valve. Such a tooth could be easily destroyed. This tooth is not always developed on specimens of the type species (Cossmann and Peyrot, 1911, p. 213).

Spaniorinus nicolleti Speden, new species (Plate 21, figs. 14–18; Plate 22, figs. 1–2)

ETYMOLOGY. With reference to its prevalence in the Lower nicolleti Assemblage Zone.

DESCRIPTION. Small, specimens 3.9 to 12.6 mm long, equivalve, inequilateral. Umbones posterior of center, insignificant, compressed, weakly prosogyrous. No lunule or escutcheon. Shape compressed subquadrangular, some variation in height to length ratio. Height,

half width and anterior length, respectively, 68.6 to 80 (N = 44, μ = 73.8%), 9.1 to 15.9 (N = 42, μ = 12.5%) and 49.6 to 56.8 (N = 44, μ = 52.4%) percent of length. Maximum height at umbone. Dorsal margin approximately straight, drops off sharply at extremities, giving an alate appearance, the posterior "wing" the more distinct. Anterior and posterior ends rounded, the latter weakly truncated below half height, the anterior narrower. Shell vitreous with very faint concentric striae and growth depressions on large specimens.

Hinge narrow, one large cardinal tooth in each valve, situated below the anterior end of the umbone. Right valve cardinal large, trigonal, pointed, strongly projecting with its ventral part curving anteriorly. Left valve cardinal smaller, conical, situated dorsally and fitting in front of that on the right valve. Resilifer internal, a wide strongly prosoclinal groove situated below umbone under the overhanging dorsal margin, bordered below by a weak to strong lamella, and separated from the cardinal tooth by a relatively broad weakly concave surface. Above and behind resilifer is a featureless broad surface. A similar smaller surface is present in front of the cardinal tooth. On the right valve the dorsal margin of these "surfaces" is bent inward to overlap and interlock with the corresponding dorsal margin of the left valve. Inflexion slight with an underlying weak groove on some specimens. No lateral teeth. No trace of impression of external ligament.

Adductor insertion areas relatively large and impressed. Anterior narrower and longer than posterior, its base situated lower than that of the posterior, elongated kidney-shaped. Posterior adductor stouter, subquadrangular, the inner margin weakly concave. Pallial line simple, remote from ventral margin, relatively broad and impressed. It continues dorsally from the adductor insertions to become indefinite near center of hinge. A narrow ridge extends from near umbone to top of anterior adductor.

Ostracum very thin, maximum thickness 0.15 mm, apparently of two layers. A very thin outer clear prismatic layer one sixth of the thickness of the shell, and an inner layer of complex cross-lamellar structure.

Types. Holotype YPM 24405, a bivalved shell, with the valves displaced and outer shell largely incomplete (Pl. 21, fig. 18), Loc. 238, Protocardia-Oxytoma Assemblage Zone. L = 9.7, H = 6.9, $\frac{1}{2}$ W = 1.2, AL = 5.4 mm. Paratypes: YPM 24408 and 24409, right and left valve steinkerns which give hinges; YPM 24407, a right valve with most of outer shell surface; YPM 24406, an internal umbonal fragment showing hinge details; YPM 24404 and 24410, steinkerns with details of musculation; and 80 other paratypes, YPM 24403, 24568–638, 24650–58.

Discussion. The conical cavity under the umbones containing the resilifer apparently does not extend to the exterior. Differences from typical species of *Spaniorinus* are enumerated above.

MATERIAL. 111 specimens, mostly (63.6%) articulated.

Occurrence. A rare species virtually restricted to the Trail City Member (96.4%) and to the Lower nicolleti Assemblage Zone (75.9%) within this member. The Protocardia-Oxytoma Assemblage Zone provided 14.5 percent. Spaniorinus nicolleti generally occurs as one or two specimens per concretion. More than three were found only in concretions from the Lower nicolleti Assemblage Zone.

COMPARISON. Spaniorinus nicolleti vaguely resembles Tellina cheyennensis Meek & Hayden which, however, has more prominent umbones, a distinct umbonal to posteroventral angulation, and is almost twice as long and more inflated.

PALEOECOLOGY. Most erycinacids are symbiotic. A few nest separately or in a symbiotic relationship (Laseron, 1956). The occurrence of 11 specimens in one concretion

(A1073) and of four or more in four others suggests that S. nicolleti may have locally followed a nesting habit.

HINDSIELLA

Auтнов. Stoliczka, 1871, р. 266.

Type Species. By original designation, Modiola arcuata Defrance (1824, p. 516), Calcaire Grossier (Eocene), Paris Basin. [non Modiola arcuata Lamarck, 1807, p. 237.]

Discussion. Corsonensis sp. n., described below, differs from typical Hindsiella in several details here considered unimportant because of the known variability of shape and hinge morphology amongst erycinacids. The ventral median sulcus is weak or virtually absent on several specimens. The cardinal tooth of the left valve is rudimentary and more or less a thickened projection of the margin, and the right valve cardinal is cylindrical and projecting. The dorsal margins are strongly incurved with a linear furrow below, especially on the right valve. The extremities of the hinge resemble those of species classed in Sportella and the central part matches that described for H. donacia Dall (1900, p. 1136).

Hindsiella corsonensis Speden, new species (Plate 22, figs. 3-8)

ETYMOLOGY. From Corson County, South Dakota, the source of most specimens.

Description. Small, specimens 5.2 to 8.8 mm long, equivalve, inequilateral, compressed. Umbones pointed, prosogyrous, moderately projecting, practically confluent with dorsal outline. No lunule or escutcheon, the anterodorsal margin in front of umbone with a marginal groove and a flanking irregular ridge. Maximum height at umbone, maximum inflation in dorsal third. Height, half width and anterior length, respectively, 66.9 to 73.1 (N = 13, μ = 70.7%), 14.0 to 19.3 (N = 12, μ = 16.9%) and 44.0 to 47.5 (N = 13, μ = 45.5%) percent of length. Anterodorsal margin straight or weakly concave, anterior and narrower, slightly tapering, rounded, continuous with convex or weakly sinuous ventral margin. Posterodorsal margin convex, posterior margin rounded, sometimes subtruncate above. Shell with faint concentric striate dorsally, becoming stronger and irregular ventrally, and sometimes with irregular weak concentric plications. A faint broad sulcus is present near middle of ventral margin on a few specimens.

Hinge line extends most of length of dorsal margin, moderately wide. A projecting cylindrical cardinal on the right valve is received in a socket on the left valve; the margin in front of this socket is thickened to represent a rudimentary left valve anterior cardinal. A weak triangular protuberance along the posterodorsal margin of the socket and under the umbone may be a rudimentary left valve posterior cardinal. Internal resilifer a weak groove extending prosoclinally subparallel to the dorsal margin from the tip of the umbone, bordered above by rounded surface of nymph. Nymph short, thin, most distinct posteriorly where the external ligament is sunken in a narrow groove. External and internal ligament apparently confluent under tip of umbone. Dorsal margins incurved, projecting more strongly on the right valve, underlain by shallow furrows. Ventral margin of hinge below furrows weakly rounded and projecting, more so on the right valve.

Adductor insertion areas subequal, weakly impressed, sited below ends of hinge in dorsal half of shell. Anterior adductor elongated rectangular, inner margin irregular,

with a dorsal short fingerlike continuation. Posterior slightly larger, suboval with a long narrow anterodorsal lobe extending halfway to end of resilifer. Pallial line simple, relatively wide and remote from ventral margin.

Ostracum less than 0.15 mm thick. Layering indefinite, inner surface exposes concentric cross-lamellar structure. Faint radial costae occur above the pallial line and concentric undulations are present on some specimens.

Types. Holotype, YPM 24414 (Pl. 22, fig. 4), a right valve with dorsal and some lateral shell, from Loc. 222, Lower *nicolleti* Assemblage Zone. L = 7.6, H = 5.4, $\frac{1}{2}$ W = 1.3, AL = 3.3 mm. Paratypes: YPM 24415, a right valve steinkern showing muscle scars; YPM 24416, a left valve shell showing hinge; YPM 24413, a right valve shell showing hinge; YPM 24412, a right valve steinkern giving hinge; and 12 other paratypes, YPM 24556-24567.

Discussion. Measurements from two bivalved specimens prove corsonensis to be equivalve.

MATERIAL. 21 specimens, mostly steinkerns, a few retaining some shell.

OCCURRENCE. As one or two single valves per concretion. Hindsiella corsonensis is essentially restricted to the Lower nicolleti Assemblage Zone (81%). The only three bivalved specimens were collected from this assemblage zone. One valve was obtained from each of four other assemblage zones.

ERYCINA

Author. Lamarck, 1805, p. 413.

Type Species. By designation under Plenary Powers (ICZN Opinion 217, 1954), Erycina pellucida Lamarck (1805, p. 414; 1806, p. 53), Calcaire Grossier (Eocene), Paris Basin.

Erycina? sp. A (Plate 22, fig. 15)

A left valve (YPM 24411) from the Timber Lake Member, Loc. 176, is tentatively placed here.

Compressed subquadrangular, length 7 mm, height and half width respectively 78.6 and 11.4 percent of length, shell with a faint broad median sulcus giving a weakly sinuous ventral margin. No lunule, escutcheon or nymph. Ornament of irregular, frequently anastomosing, weak raised concentric striae and faint irregular radial striae. Umbone small, projecting, incurved and opisthogyrous. Left valve hinge very narrow. Cardinal teeth weak, under umbone. A small posterior lamellar tooth under the umbone is separated by a broad flat area from a stronger anterior tooth. Below the anterior cardinal, and weakly separated from it, there appears to be a small raised ridge which parallels the ventral margin of the hinge. Posterior and anterior dorsal margins gently convex, thin, strongly incurving over a prominent furrow, probably the socket for lateral teeth of the right valve. Ventral margin below furrow not thickened or projecting. Socket for ligament possibly internal, a narrow furrow under dorsal margin behind the posterior cardinal tooth. Other internal morphology unknown.

LUCINACEA

EPILUCINA

Author. Dall, 1901, p. 806.

Type Species. By original designation, Lucina californica Conrad (1837, p. 255, Pl. 20, fig. 1), Upper Pliocene to Recent, California (Grant and Gale, 1931, p. 286).

Discussion. Dall originally proposed the taxon as a section of *Callucina* Dall (1901). It was transferred to the subgenus *Lucina* (*Myrtea*) by Grant and Gale (1931, p. 285), made a subgenus of *Codokia* by Chavan (1937, p. 272) and raised to generic rank by Keen and Frizzell (1939, p. 15).

A thorough revision of Upper Cretaceous lucinoid taxa is required before many species can be placed with certainty. Because of the overall similarity of external and internal morphology, cedrensis is placed tentatively in Epilucina, although its posterior laterals are weak and situated on the posterodorsal margin of the hinge above the end of the sunken ligament in contrast to the stronger posteroventrally sited laterals of E. californica. Saxolucina (Stewart, 1930, p. 184), Jurassic to Recent, is similar in shape and ornament and in the position of weak posterior lateral teeth on the posterodorsal margin of the hinge above the end of a deeply sunken ligament. It differs in the weakness and position of the anterior lateral teeth and in possessing a deep large lunule on each valve. Codalucina Stewart (1930, p. 184), considered by Chavan (1938, p. 68) to be conspecific with Saxolucina, is distinguished from cedrensis by its lack of lateral teeth, except perhaps for traces of weak anterior laterals, and possession of a more prominent lunule. Plastomiltha Stewart (1930, p. 191) lacks lateral teeth and has a longer anterior adductor insertion area which is situated closer to the pallial line.

Epilucina? cedrensis (Stanton) (Plate 22, figs. 9-11)

Lucina occidentalis (Morton). Stanton, 1914, p. 352. Lucina cedrensis Stanton, 1920, p. 30, Pl. 13, figs. 10a,b; 11a,b. Miltha (Plastomiltha) cedrensis (Stanton). Cvancara, 1966, p. 334, Pl. 8, figs. 8, 9, 12; fig. 5.

Description. Specimens 20 and 30 mm long, equivalve, inequilateral, compressed, umbones small, not prominent, prosogyrous. Lunule small, narrow, impressed and asymmetric. No escutcheon. Shape subquadrangular with a high arched posterodorsal margin, a truncated posterior margin, and an asymmetrically rounded anterior margin. A posterodorsal area is vaguely defined by a weak ridge extending from the umbone to posteroventral angulation. Height, half width and anterior length, respectively, about 95, 20 and 45 percent of length. Shell ornamented by fine concentric striae and irregular growth lamellae.

Hinge line occupies about three quarters of dorsal margin, arched, narrow anteriorly, wide posteriorly, heterodont, the cardinal teeth displaced forward by the depressed nymph and large ligament area. Dental formula

AI 3a 3b PI PIII AIV AII 2b 4b PII PIV

AI large and pointed, situated under end of lunule; 3a small, partially fused to lunular margin; 3b larger, trigonal with a weak central groove. AII large and elongated, sepa-

rated from a smaller AIV by deep socket; posterior end of AIV poorly differentiated from lunular margin; 2b large, trigonal, weakly bifid; 4b lamellar, separated from nymph by a broad shallow socket. Posterior laterals remote, sited posterodorsally above ligament area at end of marginal plate. Nymph sunken, narrow, highest and widest posteriorly. Ligament sunken, exposed externally for anterior third of length, its attachment area grooved, defined dorsally by ridge and overlain by a smooth area.

Heteromyarian, adductor insertion areas impressed. Posterior insertion smaller than anterior, subquadrangular, under posterior laterals. Anterior with a small oval dorsal catch part and a short elongated ventral portion only slightly divergent from the pallial line. Pedal retractor insertion areas small, elongate-oval, discrete, situated close to internal dorsal margin of adductor, the anterior strongly impressed. Pallial line simple. A line of pallial attachment extends from anterior pedal insertion into umbonal cavity where there are two or three swollen impressions under cardinal teeth. Anterior and posterior ridges for attachment of gills and line of pallial blood vessel are distinct.

Ostracum up to 2 mm thick, of two layers, an outer of concentric cross-lamellar structure and an inner of complex cross-lamellar structure. Outer surface of inner layer apparently radially costate. Inner surface of ventral margin apparently smooth.

Types. Of Lucina cedrensis Stanton, USNM 32406, by original designation, a left valve shell incomplete posteroventrally, L=c.37, H=c.33, 1/2 W=8.8 mm. Type locality: north of Cedar River, about 10 miles southwest of Pretty Rock, North Dakota. Stratigraphic position: Cannonball Formation, Paleocene.

Types held at YPM are: hypotypes YPM 24435-36.

MATERIAL AND OCCURRENCE. Three single valves from the Tancredia-Ophiomorpha Biofacies, Loc. 83.

Comparisons. Stanton's (1920) specimens from the Cannonball Formation, North Dakota, although larger, have the same proportions and do not show any morphological differences. The hinge characters are almost identical. *Epilucina? cedrensis* is readily distinguished from *Nymphalucina occidentalis* (Morton) by its compression and characteristics of the posterodorsal margin.

NYMPHALUCINA, new genus

ETYMOLOGY. Nympha (latin), a nymph or bride, feminine; and Lucina. Referring to a Lucina with a strong nymph.

Type Species. Here designated, Tellina occidentalis Morton (1842, p. 210, Pl. 11, fig. 3), Western Interior, U.S.A., Maestrichtian.

Diagnosis. Adult large, with weakly defined posterior and anterior areas, lunule lanceolate, moderately impressed, escutcheon narrow and extends the length of the posterodorsal margin. Shell ornamented with fine concentric striae and growth lamellae, and the internal margin below pallial line with faint, coarse, widely spaced crenulations that are strongest and often distinct only anteriorly.

Hinge AI 3a 3b PI AIV AII 2b 4b PII PIV; cardinals strong and projecting, 3a large, pointed, and separated from margin by a socket, 3b and 2b weakly bifid, 4b narrow, long, and continuous with the lunular margin. Lateral teeth extremely isolated from the cardinals and near extremities of dorsal margin, elongated; AI, PI, AIV and PII strong. Nymph long and strong, extends for about three quarters of the length of the posterodorsal margin, and the posterodorsal end sometimes projects above shell margin. Ligament

opisthodetic, external. Anterior muscle insertion area club-shaped, with a narrow posteroventral elongation diverging from pallial line and extending to about mid-height of shell.

Discussion. The hinge notation above is based on Bernard (1895–97) as modified by Douvillé (1921) and Casey (1952). The distinctive generic characters are the strength of the cardinal teeth, especially of 3a and its isolation from the dorsal margin, the isolation and strength of the lateral teeth, which are separated from the cardinals by relatively featureless plane surfaces, and the very large, strong and long nymph that supports an external ligament. Together these and the external form differentiate Nymphalucina from any other lucinoid genus. It is closest to Jagonoma Chavan (1946, Jurassic to Thanetian of Europe), which has a weak, short sunken nymph and ligament, the anterior lateral teeth closer to the cardinal teeth, regular strong concentric lamellae, and a short anterior adductor scar that diverges only slightly from the pallial line. Jagolucina Chavan (1937), Jurassic, originally placed close to Jagonia Recluz and later considered (Chavan, 1946) more closely related to Miltha and Saxolucina, has more remotely situated anterior lateral teeth and a larger nymph than Jagonoma, but the laterals are closer to the cardinals and the nymph is small when compared to Nymphalucina. The cardinal teeth 3b and 2b of Jagolucina are strongly bifid.

Two small species may be congeneric with N. occidentalis. Lucina dentonana Stephenson (1952), from the Woodbine Formation, Texas has a similar hinge and ligament. The hinge of Lucina linearia Stephenson (1941), from the Navarro Group, Texas is also similar, but the nymph appears to be less prominent, the lunule is impressed and the anterior laterals are less remote. The last two features may be of specific importance only.

Nymphalucina occidentalis (Morton) (Plate 22, figs. 12–14; Plate 23, figs. 1–7, 10–13; Plate 24, figs. 1–7)

Tellina occidentalis Morton, 1842, p. 210, Pl. 11, fig. 3.

?Lucina Owen, 1852, Pl. 7, fig. 8.

Lucina occidentalis (Morton). Meek & Hayden, 1856c, p. 273. Meek, 1876, p. 134, Pl. 17, figs. 4a-d. Whitfield, 1880, p. 409, Pl. 11, figs. 19–20. Whiteaves, 1885, p. 39.

Lucina subundata Hall & Meek, 1856, p. 382, Pl. 1, figs. 6a-b. White, 1877, p. 184, Pl. 18, fig. 12a. Meek, 1876, p. 133, Pl. 17, figs. 2a-e. [?]Stanton, 1893, p. 97, Pl. 22, figs. 5, 6.

Lucina (Diplodonta?) subundata Hall & Meek. Whitfield, 1880, p. 411, Pl. 11, figs. 17, 18.

Lucina ventricosa Meek & Hayden, 1860b, p. 427 (nomen nudum). Whitfield, 1880, p. 410, Pl. 11,

figs, 14-16.

L. occidentalis var. ventricosa Meek & Hayden. Meek, 1876, p. 135, Pl. 17, figs. 3a-c.

[?]L. profunda White, 1881, p. 158-159. White, 1882, p. 138, Pl. 1, figs. 5, 6.

[?]L. cleburni White, 1882, p. 139, Pl. 1, figs. 3, 4.

[?]L. juvenis Stanton, 1893, p. 98, Pl. 22, figs. 2-4.

Description. Length of specimens 2.6 to 48 mm; adult large, equivalve, inequilateral, moderately inflated. Umbones anterior of middle, inconspicuous, prosogyrous. Lunule long, narrow, lanceolate, moderately impressed, bordered by sharp angulations, marked with growth striae. Escutcheon narrow, extends the length of the posterodorsal margin. Shape suborbicular to subquadrangular with a weak to strong anterior truncation situated in dorsal two thirds of height and a distinct to strong posterior truncation in ventral two thirds of height. Basal margin rounded, posterodorsal margin straight or weakly convex, anterodorsal margin concave. Shape variable, especially the inflation, height to length ratio, and the prominence of the truncations and their associated angulations and sulci that weakly define dorsal "areas". Height, half width, anterior length, length of escutcheon and height of base of anterior extremity are, respectively, 78.1 to 93.2 (N = 70, μ = 85.9%), 16.6 to 26 (N = 70, μ = 20.8%), 35.4 to 47.8 (N = 69, μ = 41.6%), 40.3 to 53.1 (N = 50, μ = 46.6%) and 30.8 to 41.3 (N = 32, μ = 35.9%) percent of length.

Small shells (less than 8 mm long) ornamented with fine concentric striae and costae, which are continuous with a thin flange that arches ventrally almost to cover the adjacent furrow (Pl. 24, fig. 6). The costae project above the dorsal margin as small triangular plates, especially posteriorly (Pl. 24, fig. 5). Adult ornamented with concentric striae and regularly or irregularly spaced fine concentric costae and irregular shallow growth-pause depressions.

Hinge and nymph of adult described above. Anterior end of nymph with a weak or strong posteroventrally directed concavity, smooth or with longitudinal striae and grooves, and on the right valve separated by a weak ridge from the socket for 4b, and on the left valve by a weak ridge and sulcus from 4b. Hinge of juvenile with weak cardinal

teeth, especially 2b and 3a (Pl. 24, fig. 7).

Heteromyarian; anterior adductor described above, the oval dorsal portion (catch) and the elongated (quick) part are marked by radial costae that are stronger on the latter. Posterior adductor smaller, kidney-shaped or suboval, with a more deeply impressed small anterodorsal bulge representing a fused posterior pedal retractor. Anterior pedal retractor small, oval, mainly discrete but sometimes weakly fused to anterior adductor, situated under the anterior end of hinge. Pallial line continuous, simple, with or without a sharp posteroventral angulation. Pallial line continues dorsally as a series of five to eight small, oval or linear, discrete insertion areas that are strongest near umbones, especially anteriorly. Interior of shell with a raised ridge extending from near base of catch part of anterior adductor toward the umbonal cavity where it becomes indefinite, and a similar ridge that extends from the base of the posterior adductor into the umbonal cavity. These ridges mark the line of attachment of the gill and are, particularly the posterior, reflected externally by the sulci (Allen, 1958, p. 427). A raised ridge, discontinuous in part and with small pits, extends anteroventrally from about the middle of the posterodorsal margin, and just above the posterior adductor, to near the tip of the anterior adductor. It reflexes to continue posteriorly on some specimens (Pl. 24, fig. 3). The ridge marks the position of the pallial blood vessel (Allen, 1958, p. 430).

Ostracum up to 3.5 mm thick, of three layers. A thin outer prismatic and partly "homogeneous" layer, thickest at the anterior end of the nymph, a thick middle cross-lamellar layer and a thick inner complex cross-lamellar layer. The outer surface of the

middle layer is costate.

Types. The location of Morton's (1842, Pl. 11, fig. 3) specimen is unknown. Museums other than those visited by me should be checked before a lectotype is chosen. Type locality: "At the great bend of the Missouri River (Lat. 43° 40′N)." Stratigraphic position: Upper Cretaceous. Lectotype of Lucina subundata Hall & Meek, here designated, the specimen shown by Hall and Meek (1856) as figure 6 of Plate 1, whereabouts unknown. Type locality: On Sage Creek, near the Cheyenne River, South Dakota. Stratigraphic position: Upper Cretaceous, Campanian. Lectotype of Lucina ventricosa Meek & Hayden, USNM 344, by subsequent designation of Meek (1876, in caption to Pl. 17, fig. 3a, under the title of L. subundata var. ventricosa). Type locality: Yellowstone River, 150 miles above mouth, Montana. Stratigraphic position: Upper Cretaceous, Campanian.

Types held at YPM are: hypotypes YPM 24424-34, 24639-40.

Discussion. Although the percentages given above are based on measurements from many concretions at several stratigraphic horizons, the extreme values are only 2 percent greater than those made from samples of 17 (A327) and 20 (A520) specimens per concretion. One or two well-developed secondary teeth are present in the sockets for cardinal teeth on several specimens (Pl. 24, fig. 4). The ventral margin of the anterior part of the hinge below the socket for the reception of the lateral of the left valve is strongly thickened and slightly projecting on some small and large right valves. It simulates a lateral tooth. Ligament material, mostly the fibrous inner ligament, is preserved on the majority of the articulated specimens. The ligament is opisthodetic with an inverted U-shaped cross-section and has the general form described by Allen (1960) for

Diplodonta. The outer layer appears to be homogeneous and is a light to dark brown color. It is thickest at the base, thins over the dorsal surface. The inner layer is nacreous, fibrous, has growth layers, and is of uniform thickness above the level of the nymphs. It thins ventrally (YPM 24640). Allen (1958) did not describe a reflexion in the pallial blood vessel although one is evident in his figure 4 of Lucina pennsylvanica (= Linga; Chavan, 1937, p. 146). A reflexion comparable to that of occidentalis is also shown by specimens of Lucinoma borealis and "Lucina" floridana Conrad in Peabody Museum collections.

Specimens from the type Fox Hills show two changes with growth. The fragile ornament of the juvenile is soon lost, and the cardinal teeth 3a and 2b, which are faintly outlined on specimens less than 7 mm long, are strong on specimens 14 mm long. Chavan (1938, p. 59) noted that some lucinids undergo hinge modifications with growth. The small specimens of occidentalis have a prominent nymph and differ from the adult in no other features.

MATERIAL. 126 specimens including 15 (12.2%) single valves.

Occurrence. All but two of the 13 specimens collected from the marine part of Timber Lake Member come from Loc. 90, where they occurred as less than five specimens in each of six concretions. None of these specimens, which match the forms subundata or ventricosa, exceed 14 mm in length and most are less than 10 mm long. Their size range overlaps that of specimens from assemblages of occidentalis from the Trail City Member. This and the growth changes indicate that they are young specimens of occidentalis. Fifty-six percent of the specimens from the Trail City Member came from Protocardia-Oxytoma Assemblage Zone, 28 percent from Limopsis-Pseudoptera Assemblage Zone and 14 percent from Lower nicolleti Assemblage Zone. Nymphalucina was a codominant in one concretion from Lower nicolleti Assemblage Zone and a dominant or codominant in six concretions at three localities in Protocardia-Oxytoma Assemblage Zone. The species otherwise occurred as less than five specimens per concretion.

In the Protocardia-Oxytoma Assemblage Zone at Locality 30 occidentalis occurred

in concretions and as randomly oriented specimens scattered through the matrix.

Comparisons. Meek (1876) was uncertain if his specimens of N. occidentalis were conspecific with Morton's specimen of "Tellina" occidentalis which has an incomplete dorsal margin. As no other species resembles occidentalis and as most specimens were collected from the same region, the flgures leave little doubt that the specimens are conspecific. Meek also considered that ventricosa and subundata probably "represented different ages of the same species" (occidentalis). Whitfield (1880) found the three species associated in several, and occidentalis and ventricosa in many collections. He used minor differences in shape to distinguish the species. Whiteaves (1885) thought it "extremely probable that L. subundata is only the young of L. occidentalis". Small specimens like ventricosa occurred together with large occidentalis in one collection (A940), are present in different concretions at several localities, and the subundata form is present in most assemblage zones. This, the growth trends discussed above, and the range of variation shown by large specimens make it clear that the three "species" are conspecific and represent different age groups.

Examination of the holotype (USNM 11469) of L. cleburni White, and of specimens (YPM 24641-42; Pl. 23, fig. 8) from "Platte River Valley, NE Colorado" shows that this species differs only by having more regular narrow raised costae on the dorsal third of the shell. These costae become irregular on the ventral part of the shell. The presence of similar ornament on the umbone of some specimens of occidentalis and of irregular ornament on the same area on some individuals of cleburni suggests that the differences may not be of specific rank and may represent phenotypic variation. Larger samples of cleburni are required to clarify the problem. Stanton (1893) stated that his specimens of L. juvensis "are not easily distinguishable from young individuals of subundata" and he doubted if the two would have been separated if they occurred together. The

ornament of L. profunda White (holotype, USNM 8362) matches that of occidentalis but it has a very narrow posterior and a wide anterior end. One small specimen (YPM 24423; Pl. 23, fig. 14) from the Elk Butte Member, Pierre Shale, tentatively identified as Lucina sp. indet., resembles profunda. Both specimens may be extreme forms of small occidentalis.

?GLOSSACEA

CLISOCOLUS

AUTHOR. Gabb, 1869, p. 188.

Type Species. By monotypy, ?Loripes dubia Gabb (1864, p. 177), Lower Asuncion Group, lower-middle Campanian (Popenoe and others, 1960), California.

EMENDED DIAGNOSIS. Orbicular to globular with a thick shell and tumid projecting umbones. Ornament of fine concentric striae, irregular costae and prominent narrow growth depressions (C. moreauensis (Meek & Hayden)), or with strong sharp-ridged costae (corrugatus Popenoe). Juveniles sometimes with faint fine radial costae (moreauensis). Dentition weak, hinge sometimes appears edentulous. One weak cardinal tooth in each valve; the right valve has a faint broad protuberance that simulates a second anterior cardinal tooth. Cardinal tooth of right valve situated behind the umbone, relatively strong, either projecting and nodular, or a weak elongated protuberance that is strongest posteroventrally. Left valve cardinal variable in size and degree of projection, nodular or elongated, situated below tip of umbone. No lateral teeth. Ligament partly external, with a posterior portion borne on short to long moderately strong nymphs, and partially shallowly to deeply sunken in a pit posterior to and below umbones. This sunken pit is continuous with a narrow, weak to strong sulcus that extends posteroventrally across the anterior end of the nymph and defines the posterior limit of the right valve cardinal tooth.

For musculation and shell structure, see below under C. moreauensis.

Discussion. The synonymy given below indicates the past uncertainty of the generic position of *C. moreauensis*. Although mostly classed under *Sphaeriola* Stoliczka, Meek (1876), Whiteaves (in White, 1889, p. 41) and White (1889) considered that the specimens from the Western Interior classed under *cordata* and *endotrachys* probably represented a new genus. Whiteaves (1879, p. 41) previously included *cordata* of Meek and

Hayden under Clisocolus Gabb, a procedure followed by Landes (1940).

The sunken ligament pit behind the umbones and dentition distinguish Clisocolus from several other externally similar genera. Shell structure, when studied for the other genera, may also prove diagnostic. Sphaeriola Stoliczka, Triassic and Jurassic, type species Cardium madridi d'Archaic (see Morris and Lycett, 1853, p. 70, Pl. 7, figs. 14, 14a-d) has two cardinal teeth in each valve, the anterior on the right valve being elongated anteriorly, and sometimes traces of laterals. Sphaera Sowerby, Jurassic and Cretaceous, type species Sphaera corrugata Sowerby, is subquadrangular in shape, has two cardinal teeth in each valve, strong lateral teeth, with as many as three posteriorly, and the nymph is short (Woods, 1907, p. 157, Pl. 25, fig. 2; Rollier, 1913, p. 239, Pl. 24, figs. 1–6; Gillet, 1924, p. 124, fig. 76). Species of Mactromya and Unicardium discussed by Chavan (1950) are compressed, subquadrangular, with anteriorly or posteriorly situated umbones, and a different arrangement of teeth. Chavan (p. 6) notes that U. (Ferreta) acesta d'Orbigny has a reduced resilial socket in front of a "large" nymph. The shape, posteriorly situated beaks and large anterior rather than posterior cardinal teeth distinguish acesta

from *Clisocolus* (see also Morris and Lycett, 1853, Pl. 8, figs. 9, 9a-c; d'Orbigny, 1843, Pl. 279, fig. 3; Gillet, 1924, p. 125, fig. 78).

Examination of four hinges (Pl. 26, figs. 9-12) of specimens of C. corrugatus Popenoe, Baker Canyon Member of the Ladd Formation, Turonian (Anderson, 1958, p. 28), Santa Ana Mountains, California shows that it is congeneric with moreauensis. Clisocolus corrugatus has the same dental pattern and sunken resilifer, although the latter is extremely variable in size, degree of depression of the resilifer, and is situated more posteriorly than on moreauensis. On one left valve (UCLA 39598, L = c.21 mm, Pl. 26, fig. 10) the pit is insignificant and not sunken (cf. C. dubia, Pl. 26, fig. 5), while on a similar-size left valve (UCLA 39596, L = c.21 mm, Pl. 26, fig. 11) it is small but distinct and slightly sunken. On larger right valves the resilifer is prominent and moderately (UCLA 39597, L = 35.5 mm, Pl. 26, fig. 12) to strongly (UCLA 39599, L = 22.5 mm, Pl. 26, fig. 9) sunken. The resilifer is strong, moderately sunken and relatively consistent morphologically on all specimens of moreauensis longer than 18 mm (YPM 24012, Pl. 25, fig. 13). The size of the resilifer relative to the remainder of the hinge indicates that it is probably present on all specimens, at least on those down to 10 mm long. The hinge of moreauensis shows marked ontogenetic changes in morphology. Small specimens (L = 3 to 7 mm, Pl. 25, fig. 10) have two prominent cardinal teeth on the right valve, and a strong anterior and a weak posterior on the left valve, but the hinges are too small to ascertain if a small resilifer is present at the anterior end of the nymph.

The hinge of the holotype of ?Loripes dubia Gabb (= Clisocolus Gabb; ANSP 4403, here refigured, Pl. 26, fig. 5; see also Whiteaves, 1879, Pl. 18, figs. 3a, b; Stewart, 1930, p. 188, Pl. 17, fig. 3), a right valve, resembles that of moreauensis but lacks a sunken resilifer at the anterior end of the nymph. The dorsal margin is indented by a shallow depression situated at the end of a furrow that defines the anterodorsal border of an elongated protuberance (3b). This depression also separates the posterior end of the anterodorsal margin from the nymph. The surface of the nymph has a shallow furrow aligned subparallel to its dorsal margin. The holotype of dubia, an incomplete specimen 10.1 mm long, and possibly 10 to 14 mm when entire, is probably a juvenile, especially as corrugatus and moreauensis reach 40 to 55 mm in length. Yet, because of the gross similarity of the hinges, the ontogenetic variation of the hinge and the resilifer, and the variation of the strength of the resilifer shown by the few specimens of corrugatus, dubia is here considered congeneric with moreauensis and corrugatus, and the name Clisocolus is applied to all three species. To confirm this step the collection of topotypic adult specimens of dubia is desirable.

Trueman (1964, p. 62) has cautioned that care should be taken in the interpretation of the subumbonal region of bivalves, as a secondary resilium may result from the fracturing of the opisthodetic ligament by tangential growth of the valves. By analogy, tangential growth may be responsible for the variability of the resilifer on specimens of *C. moreauensis* and *corrugatus*, and the posterior migration of the pit as the umbone of moreauensis is etched away during life. Consequently, the resilifer is possibly largely a secondary feature and of minor importance for systematic classification.

Clisocolus has been placed in the Glossacea (= Isocardiacea; Popenoe, 1937; Landes, 1940), in the Tellinacea (Unicardiidae; Chavan, 1950), in the Lucinacea (Mactromyidae; Ichikawa and Maeda, 1966), or considered to be of unknown position (Stewart, 1930). The gross form of the shell, the incurved and out-twisted umbones, musculation and pallial line, prominence of the nymph, and the elongation of the most strongly developed teeth parallel to the hinge margin favor classification in the Glossidae. Clisocolus differs primarily in the weakness of its sunken resilifer, dentition and the lack of lateral teeth. The oval inflated shape and simple pallial line of Clisocolus are not compatible with the mobile deposit-feeding mode of life followed by most tellinids. Classification must remain uncertain until more is known of genera classed in the above taxa.

Ichikawa and Maeda (1966) recorded a new species of *Clisocolus, C. crenulatus*, from the Izumi Group (Campanian and Maestrichtian) of Japan. Because of its possession of strong marginal crenulations, the species was placed in a new subgenus *Crenocolus* Ichikawa.

Clisocolus moreauensis (Meek & Hayden) (Plate 24, figs. 8–11; Plate 25, figs. 1–13; Plate 26, figs. 6–8)

Cyprina cordata Meek & Hayden, 1857, p. 143; non Cyprina cordata Sharpe, 1850, p. 182.

Bucardia? moreauensis (Meek & Hayden). Meek & Hayden, 1860b, p. 427.

Glossus? moreauensis (Meek & Hayden). Gabb, 1861, p. 125.

[?] Sphaeriola obliqua Meek, 1875, p. 46.

Sphaeriola? cordata (Meek & Hayden). Meek, 1876, p. 137, Pl. 29, figs. 3a-c. Kellum, 1962, p. 62, Pl. 3, figs. 1, 2.

*\$ 27.19 1°

Sphaeriola? warrendna Meek, 1876, p. 138.

Sphaeriola? endotrachys Meek, 1876, p. 139, Pl. 29, fig. 2.

[?]Sphaeriola transversa Whitfield, 1877, p. 34; 1880, p. 415, Pl. 10, figs. 14-16.

Clisocolus moreauensis (Meek & Hayden). Landes, 1940, p. 155.

Clisocolus endotrachys (Meek). Landes, 1940, p. 154.

[?] C. transversa (Whitfield). Landes, 1940, p. 155.

DESCRIPTION. Length of specimens 3.2 to 46.3 mm, few less than 25 mm, equivalve, inequilateral, very tumid with maximum inflation about two thirds of height. Umbones anterior of center, extremely prominent, projecting, prosogyrous, and incurved. Shape variable, orbicular to globular. Height 90.6 to 105.6 (N = 45, μ = 96.9%), width of one valve 29.2 to 43.9 (N = 45, μ = 34.7%) and anterior length 37.1 to 47.1 (N = 44, $\mu = 41.4\%$) percent of length. Posterodorsal extremity angulated, anterodorsal rounded. Escutcheon one half to two thirds of the length of posterodorsal margin; no lunule. Ornamentation, hinge and ligament described above. Dimyarian, adductor insertion areas very large, their base situated at or just below half the height of shell, moderately impressed, subequal. Anterior adductor insertion larger, elongate-oval, with the anterodorsal extremity (anterior pedal retractor) extending as a narrow band for several millimeters under the buttressed anterior end of hinge. Posterior insertion subcircular, more deeply impressed, joined by a narrow pallial band to a deeply impressed, small, elongate-oval posterior pedal insertion situated under the buttressed posterior end of hinge. A small oval (pedal retractor) is situated under the hinge on "the posterior side of the base of the umbonal cavity. Pallial line simple, relatively wide, with a small posteriorly directed sinus where it joins the posterior adductor.

Ostracum of three main layers. An outer punctate concentric cross-lamellar layer, a middle concentric cross-lamellar layer and an inner dominantly complex cross-lamellar layer.

Types. Lectotype of Cyprina cordata Meek and Hayden, USNM 457, by subsequent designation of Meek (1876, in caption to Pl. 29, fig. 3a), an articulated specimen with some shell, margins incomplete, L = c.42, H = c.41, $\frac{1}{2}$ W = c.18, AL = c.16.5 mm. Type locality: "Moreau River, No. 5 of the series", South Dakota. Stratigraphic position: probably from the Fox Hills Formation, possibly the Trail City Member. Lectotype of Sphaeriola? endotrachys Meck, USNM 12385, by subsequent designation of Meek (1876, in caption to Pl. 29, fig. 2), a bivalved steinkern, the posterior and ventral margins incomplete and replaced by plasticene, L = 38.0, H = 37.5, W = 29.5, AL = 14.5 mm. Type locality: "ninety miles below Fort Benton, on the Missouri". Stratigraphic position: [?]Fox Hills Formation. Lectotype of Sphaeriola? warrenana Meek, USNM 458, here designated, the only specimen, bivalved and gaping, the right valve a steinkern, the left valve with shell on dorsal half and showing part of hinge, L = c.39, H = c.37.5, W = c.33.5, AL = c.17.5 mm. Type locality: "near the eastern base of the Black Hills, South Dakota." Stratigraphic position: "Fox Hills" Formation. Lectotype of Sphaeriola transversa Whitfield (1877, USNM 13215, here designated, the original of figures 14 and 15, Plate 10 (Whitfield, 1880), a two-valved steinkern with some shell, the largest specimen known to me, L = 51.0, H = 45.8, $\frac{1}{2}$ W = 18.6, AL = 19 mm. Type locality:

Cheyenne River, near Old Woman Fork, Wyoming. Stratigraphic position: Fox Hills Formation, ?Maestrichtian.

Types held at YPM are: hypotypes 24009–13, 24014–19.

Discussion. The umbonal region of most specimens was deeply etched during life (Pl. 25, fig. 12). Sometimes much of the central part of the hinge is destroyed and the sunken ligament pit and nymph are displaced posteriorly (Pl. 25, fig. 12). The displacement suggests that when necessary the shell was resorbed. A thin brownish layer of homogeneous or granular structure covers the ligament of several specimens and is also present anterior to the umbones. On one specimen (YPM 24015) it is continuous with a similar light-brownish layer, the periostracum, covering the anterodorsal margins of the valves (cf. Glossus humanus Linnaeus; Owen, 1953).

The punctate outer shell layer weathers to a characteristic honeycomb structure. The position of the pallial line indicates that the myostracum lies within the inner shell layer. This inner layer is mainly complex cross-lamellar in the umbonal region, but concentric cross-lamellar structure is commonly present near the ventral margin. Some steinkerns show a pitted surface especially on the upper half. Whiteaves (1879) thought it was due to disease. Meek (1876, p. 139) and Landes (1940) used this "roughness" of the interior of the shell as a diagnostic feature of S. ?endotrachys. Specimens of both forms, moreauensis supposedly having a thicker shell and no protuberances, here considered to belong to one species, show this pitting. The raised oval to elongate areas on the inside of the shell apparently coincide with concentric cross-lamellar areas (Pl. 25, fig. 3). These projections are emphasized by the extent to which the surrounding shell breaks away during separation from the steinkern.

MATERIAL. 122 specimens, mostly articulated.

Occurrence. The species is virtually restricted to the Trail City Member, with 67.2 percent of specimens from Lower *nicolleti* Assemblage Zone and 26.2 percent from the *Protocardia-Oxytoma* Assemblage Zone. Articulated valves dominate. Only six concretions contained more than one specimen. Two concretions at Loc. 219 had four specimens. Most are well preserved being secondarily damaged by weathering and extraction. Only one specimen was positively broken prior to burial.

There are few records, other than those given above, of C. moreauensis from Upper

Cretaceous sequences of the Western Interior.

Comparisons. Meek (1876) listed three species, C. moreauensis, endotrachys and warrenana, from localities in the Fox Hills Formation of western South Dakota and eastern Wyoming. The measurements given by Meek are incorrect. All "holotypes" have similar measurements which correspond closely to the average values calculated for specimens from the type area of the Fox Hills. Measurement of a suite of eight of Landes' (1940) specimens, kindly forwarded by Dr. J. A. Jeletzky, from the Bear Gulch Member of Pakowki Foundation gave height to length ratios of 94 to 101 percent. This, and the other ratios fall within the range of variation of the Fox Hills specimens. Landes' specimens differ only in having more coarse costation on the ventral half of some individuals and a narrower and more inward-projecting nymph (Pl. 25, fig. 3). Although of the same dimensions, the type specimen of S. obliqua Meek (USNM 7835) is too poorly preserved to be sure of its specific relationships. Whitfield (1880) considered S. transversa to have larger and more incurved umbones than moreauensis. Measurements of the original specimens (USNM 12315, 12316) show that the shape does not differ, nor does the musculation, and the left valve hinge figured by Whitfield (1880, Pl. 10, fig. 16; USNM 12316) was idealized by the artist and is based on a cast from a poorly preserved steinkern. It is indistinguishable from moreauensis.

As the four species, Clisocolus moreauensis, warrenana, endotrachys and transversa, come from different stratigraphic levels and geographic areas, synonymy, although

probable, cannot be considered proven until biometric studies on fossil populations have been undertaken.

Three species of Clisocolus, dubius, corrugatus Popenoe and "cordatus" of Whiteaves (1879, p. 157), have been named from the upper Cretaceous of the Pacific coast. The last two closely resemble the Western Interior moreauensis in size, shape and shell structure. Through the kindness of Dr W. P. Popenoe, University of California at Los Angeles, I have been able to examine specimens of corrugatus and "cordatus". The oldest species, corrugatus, from the Baker Canyon Member of Ladd Formation, Turonian, Santa Ana Mountains, differs from moreauensis by the presence of narrow strongly projecting costae, even on the umbones, the variation in the presence or absence of the sunken resilifer, and the greater strength of an elongated cardinal protuberance behind the umbone on the right valve (Pl. 26, figs. 9, 11). Clisocolus "cordatus" specimens from Cedar District Formation, Sucia Island, Upper Campanian, and the Pleasants Sandstone Formation, Santa Ana Mountains, Upper Campanian also have a resilifer of varying degree of depression, but differ from corrugatus and moreauensis mainly by the ornament which consists of very fine relatively regular costae on the umbonal region and also over most of the shell even when growth depressions and coarser costae are present, and by their more projecting and proportionally narrower prosogyrous umbones which tend to curve outward at the tip (Pl. 25, fig. 16; Pl. 26, figs. 1-5). C. "cordatus", like corrugatus, has a stronger cardinal protuberance on the right valve than does moreauensis. The status of dubius, which is based on a juvenile, is uncertain. Externally and internally it closely resembles small specimens of "cordatus" from Sucia Island (UCLA 39475-76, Pl. 26, figs. 1-3) and may prove to be conspecific with "cordatus" as thought by Whiteaves (1879). C. dubius Gabb was later considered by Whiteaves (in White, 1889, p. 41) to be probably distinct from the Sucia Island "cordatus". Dr. Popenoe (letter, 16 July, 1964) is "fairly confident" that they are the same, and I would not care to distinguish equal-size specimens. As the juvenile holotype of dubius, the only specimen, came from a mine shaft, now filled-in, in a valley, the collection of adult specimens from "Texas Flat" is unlikely (Dr. Popenoe, pers. comm.).

When Whiteaves (1879, p. 157) originally described the Namaimo River and Sucia Island specimens he placed them under "Clisocolus cordatus, Meek & Hayden, (Sp.)", and synonymized dubius with "cordatus". As a junior primary synonym the name cordatus is not available and the specimens should have been called moreauensis. White (1889) considered the Sucia Island species to be different from the Western Interior moreauensis and called it cordatus Whiteaves, a name accepted ever since. As Whiteaves credited the name to Meek and Hayden, it is not available and the species should have been renamed. Is the name dubius acceptable or should a new name be proposed? Although the holotype of dubius cannot be distinguished from juveniles of "cordatus", the lack of adults prevents an objective decision. The fossils are of approximately the same age, Upper Campanian (Popenoe and others, 1960), occur in similar muddy silts or sands but are separated by about 1000 miles, more than ample for specific differentiation, especially as several species of one genus may occur even in one bay (e.g. Nucula spp., Allen, 1954). Favoring acceptance of the name dubius is the advantage of not introducing a new name into the literature, the possibility of applying a new name to the Sucia Island population if it proves to be different, the similarity of the juveniles, the occurrence of only minor changes in hinge details once specimens of moreauensis exceed 8 to 10 mm in length, and the practical fact that "sibling" species are rarely able to be distinguished in the fossil record. I here propose the allotment of the name dubius to the Upper Campanian Clisocolus species of Sucia Island and the Santa Ana Mountains.

CARDIACEA?

TANCREDIA

Author. Lycett, 1850, p. 407, 424.

Type Species. By subsequent designation of Morris and Lycett (1853, p. 91) Tancredia donaciformis Lycett (1850, p. 424), Bajocian (Middle Jurassic), England.

Discussion. Saul and Popenoe (1962) discussed the systematic position of the family Tancrediidae and concluded that it was perhaps best classed in the Cardiacea rather than the Tellinacea (Chavan, 1950). Their suggestion that Chavan's Tellinacea includes stocks just as closely related to other superfamilies is probably valid. The hinge structure of Tancredia is more cardiid, and the strong posterior gape of many species and the pattern of muscle scars is against classification in a lucinoid or tellinid stock. The inhabitation by Tancredia americana of an inshore high energy environment, one comparable to the beach environments populated by the tellinid Donax, suggests the possibility of adaptive convergence toward tellinid characteristics (see also Chavan, 1950, p. 16).

Chavan raised the five groups of Tancredia recognized by Cox (1929) to subgeneric rank, and with some hesitation placed T. americana, described below, in the subgenus Corburella Lycett. T. americana has all the characters listed for Tancredia sensu stricto, namely, 3a distinct from the anterior lateral, a strong 4b, a posterodorsal angulation (reflecting the wide gape), and a weakly delimited lunule. It also has a thick hinge and strong teeth, supposedly diagnostic of Corburella, but these are considered of species rather than subgeneric rank, especially as T. donaciformis, the type of Tancredia, has these

characteristics.

Tancredia americana (Meek & Hayden) (Plate 27, figs. 1–16; Plate 28, figs. 1–8, 14)

Hettangia americana Meek & Hayden, 1856c, p. 274.

Tancredia americana (Meek & Hayden). Meek & Hayden, 1860a, p. 185; 1861, p. 426. Meek, 1876, p. 142, Pl. 38, figs. 1a-h. White, 1879a, p. 182. Whiteaves, 1885, p. 39; 1889, p. 175. Landes, 1940, p. 153. Chavan, 1950, p. 12. Saul & Popenoe, 1962, Pl. 1, figs. 3, 4.

Tancredia americana var. cupressensis Landes, 1940, p. 154, Pl. 4, fig. 8.

DESCRIPTION. Length of specimens c.5 to 61.8 mm, equivalve to slightly inequivalve with either valve up to one percent shorter or longer than the other and the right valve up to 1.3 percent lower than the left valve, inequilateral, moderately inflated, the umbones medial, prominent but flattened, weakly prosogyrous. Shape variable, subtrigonal, the anterior end tapering to a narrowly or broadly rounded extremity, the anterodorsal margin straight or slightly concave, the anteroventral margin weakly convex or faintly sinuous. Posterior end broad, truncated, the posterodorsal margin convex, the posterodorsal angulation sharp to rounded, truncated margin convex to concave, the inner margin of the posteroventral angulation often thickened. Maximum inflation about mid-height, posterior to umbones and tapers rapidly anteriorly. Posterior gape wide to very wide, extending from posteroventral angulation to end of hinge. Valves also with a slight anterior gape, most marked on small specimens which may have ends of valves twisted outward, and with a slight gape under the anterior end of the protuberance in front of the umbone of the right valve. Height, inflation of one valve, anterior length, length of nymph and length of posterior part of hinge from umbone to end of laterals, respectively, 64.4 to 81.9 (N = 157, $\mu = 72.5\%$), 20 to 31.7 (N = 157, $\mu = 26.6\%$), 45.3 to 56.3 (N = 157, μ = 51%), 12.7 to 20 (N = 129, μ = 15.9%) and 18.3 to 26.7 (N = 135, $\mu = 22.6\%$) percent of length, and posterodorsal angulation at 58.3 to 71.6 (N = 155, $\mu = 65.4\%$) percent of height. Area inside ridge from umbone to anterior extremity flat to inclined downward, most steeply on the left valve; escutcheon wide, open posteriorly. Shell ornamented with faint concentric striae and irregularly spaced growth lamella and depressions. A weak sulcus extends from umbone to posteroventral angulation, and the area above this is often very arched and with crowded striae (Pl. 27, fig. 1).

Hinge formula:
$$\frac{\text{(AIII)}}{\text{(AIV)}} \frac{\text{AI 3b 3a PI PIII}}{\text{(AIV)}} :$$

3a a rounded protuberance, opisthoclinal, thin and distinct on juveniles, but tends to become overgrown by a prominent boss on margin of right valve; 3b large, triangular and pointed. Posterior laterals short and narrow, on either side of a broad socket, and anterior laterals long and thin, separated from 3a by a smooth surface below the boss, with AIII the thickened margin below which is a narrow groove for the thin margin (AIV) of the left valve. Posterior cardinal (4b) of left valve at end of nymph, small but distinct, prosoclinal, relatively prominent on small specimens; 2 is large, pointed, triangular, the valve margin in front of umbone has a broad indentation for reception of 3a and the boss of right valve, and the margin projects vertically as a narrow flange. Posterior lateral a large rounded protuberance, the anterior laterals weak, respectively the thin margin of the valve and the thickened ventral margin of the socket for AIII of the right valve. Ligament external, borne on short nymphs which extend from umbone to posterior laterals and have a lightly concave dorsal surface.

Heteromyarian, the anterior adductor insertion area the smaller, pear-shaped and elongated parallel to hinge margin, deeply impressed, continuous with an elliptical insertion area (pedal protractor) situated above and under the posterior end of the lateral teeth (Pl. 28, fig. 7). Posterior adductor weakly impressed, situated behind lateral teeth, narrow, elongated vertically, tapering dorsally and continuous with a narrow curving posterior pedal retractor insertion that extends under hinge to the anterior end of posterior lateral teeth. Pallial line relatively wide, broader above the posteroventral angulation where it may continue with uniform width to base of the posterior adductor, widen continuously, or have a secondary swelling fused to base of adductor (Pl. 28, fig. 1). Posterior to the anterior pedal protractor is a small oval deeply impressed insertion (pedal retractor), and situated in the umbonal cavity is a hook-shaped insertion (an elevator) opening to the rear.

Ostracum up to 4.5 mm thick, of two layers, a very thin outer homogeneous or granular clear layer, and a thick inner homogeneous whitish calcitic layer (see also Bøggild, 1930).

Types. Lectotype of *T. americana*, USNM 186, by subsequent designation of Meek (1876, in caption of Pl. 38, fig. 1b), a left valve that is incomplete anteriorly. Not located. Type locality: mouth of Judith River, Montana. Stratigraphic position: Judith River Formation, Campanian.

Types held at YPM are: hypotypes YPM 24172, 24378-83, 24385, 24699, 24701-06; other types, 24384 and 24700.

Discussion. That the slight differences in size of the valves is not due to compaction or measurement error is indicated by the consistently greater height of the left valve, the common occurrence of the right valve's becoming equal to the left valve anteriorly, and the excellent preservation of the specimens. The range of variation shown by a sample of 115 valves from Loc. 83 encompasses measurements made on smaller samples from all other localities. Of common occurrence are secondary thin raised pads on the socket-facing surfaces of the cardinal teeth. These pads are layered, do not continue around the ends of the teeth but have steep boundary faces (Pl. 28, fig. 7). They exfoliate readily and expose a chalky surface. These secondary deposits may be analogous to the vincula described by Casey (1952, p. 124).

The interpretation of the muscle insertion areas given above is based on anatomical studies of Pelseneer (1891, 1911) and others which show that heterodont genera frequently have the protractor muscle near or fused to the dorsal end of the anterior adductor and below a pedal retractor muscle as, for example, in *Corculum hemicardium* (Linneaus) and *Mesodesma complanata* (Pelseneer, 1911, Pl. 21). Also, when both the pedal protractor and retractor are present it is characteristic of bivalves that the latter is the more strongly impressed. The modifications of the vertical part of the pallial line below the posterior adductor scar is undoubtedly related to siphonal muscle attachment which is normally present in genera with siphons, for example, *Cardium edule* (John-

stone, 1899, Pl. 2, fig. 10), especially those with a wide gape and long siphons, e.g. *Panopea* and *Laternula* (Pelseneer, 1911, Pl. 24, figs. 1, 3).

The umbones of many specimens are slightly worn. A large number have hollow swellings, some with external holes, on the inner shell surface, generally near the pallial line and at the base of the adductor scars. These swellings rarely occur in the umbonal region. They resemble protuberances caused by the marine bristle-worm *Polydora*. One heavily infested specimen shows displacement of growth lines.

MATERIAL. 28 articulated specimens, 235 single valves, mainly in a selected sample from Loc. 83. The paucity of articulated valves is artificial and is due to exposure by weathering agents.

Occurrence. Tancredia americana is characteristic of, and forms shellbeds only in the Tancredia-Ophiomorpha Biofacies of the Timber Lake Member, in which it also occurs as scattered single and articulated valves. One specimen was collected from the Bullhead lithofacies at Loc. 224, one from the Colgate oyster bed at Loc. 16, and two from the banded section at the top of the Trail City Member at Loc. 121. Along the western part of the Grand River the species occurs (25.5%) in the Cymbophora-Tellinimera Assemblage Zone scattered through the matrix and in small concretions associated with Cymbophora in a muddy brownish-gray graywacke of Irish Creek lithofacies. Inadequate sampling of the Tancredia-Ophiomorpha Biofacies overemphasizes the proportion occurring in the Cymbophora-Tellinimera Assemblage Zone.

The species has been recorded from sandstone, generally resembling that of *Tancredia-Ophiomorpha* Biofacies, and sometimes associated with *Ophiomorpha*, in the Western Interior by Stanton (1893, p. 27) and White (1879a, p. 178, 182) and in south-central Canada by Whiteaves (1885, p. 39; 1889, p. 175) and Stott (1963, p. 113).

COMPARISON. No other fossil in the Upper Cretaceous of the Western Interior resembles this distinctive species.

CARDIACEA

GRANOCARDIUM

Subgenus ETHMOCARDIUM

Author of Genus. Gabb, 1869, p. 266.

AUTHOR OF SUBGENUS. White, 1880a, p. 292.

Type Species of Subgenus. By original designation of White (1880a, p. 292), Cardium speciosum Meek & Hayden, 1856c, p. 274 (non Adams & Reeve, 1850, p. 77; = C. (E.) whitei Dall, 1900a, p. 1074), Upper Cretaceous, Western Interior, U. S. A.

Discussion. *Ethmocardium*, originally proposed as a subgenus of *Cardium* by White, was raised to generic status by Marwick (1944). Keen (1954) includes it as a subgenus of *Granocardium*, and her nomenclature is followed here. In her diagnosis Keen does not record the presence of fine radial costae. However, they occur on some well-preserved shell fragments from Loc. 224.

Granocardium (Ethmocardium) aff. G. (E.) whitei (Dall) (Plate 28, figs. 9-11)

Cardium speciosum Meek & Hayden, 1856c, p. 274.

Cardium (Criocardium) speciosum Meek & Hayden. Meek, 1876, p. 169, Pl. 37, figs. 4a-c.

Cardium (Ethmocardium) speciosum Meek & Hayden. White, 1880a, p. 292.

Cardium (Ethmocardium) whitei Dall, 1900a, p. 1074.

Ethmocardium whitei (Dall). Marwick, 1944, p. 259.

Granocardium (Ethmocardium) whitei (Dall). Keen, 1954, p. 7.

Description. Specimens small, subquadrate, less than 15 mm high, height and half width respectively about 120 and 30 percent of length. Shell ornamented by 40 to 45 prominent costae which on the flanks are narrower, more projecting and asymmetric, with the shorter and steeper face toward the center of the disc. Crest of costae rounded, sharp or beveled. Costae weak on posterodorsal flank of umbone. Interspaces as wide as costae, with three to four pits per millimeter in floor of first 12 to 15 interspaces anterior to the umbonal to posteroventral angulation. Pits appear 1 to 2 mm from the smooth prodissoconch, become smaller ventrally and cease 1 to 3 mm from the ventral margin. Pits apparently covered internally and externally by thin shell layers. Costae and interspaces with weak, secondary radial costae. Concentric striae faint and most numerous on floor of interspaces, thickened on the gently sloping side of costae, generally absent from crest of costae.

Hinge relatively massive, slightly arched, heterodont, dentition of left valve known. Anterior and posterior laterals (AII and PII) strong, projecting, separated from cardinals by flat or slightly concave hinge plate. Anterior cardinal (2a) strong, trigonal, separate from dorsal margin; posterior cardinal lamellar small and short, has one or two ventral plaits, attached to end of nymph. Right valve formula probably AI AIII 3a 3b PI ?PIII; cardinals strong. External ligament borne on a short strong nymph. Musculation unknown.

Ostracum thin, apparently of two layers, an outer concentric cross-lamellar and an inner complex cross-lamellar layer. Inner surface of interspaces between pits raised or depressed. Pits are sometimes surrounded by a small raised rim. Ventral margin with strong, broad, flat-topped, square-tipped crenules, corresponding to the radial sulci, separated by narrower steep-sided notches.

Types. Lectotype of Cardium speciosum, USNM 190, by subsequent designation of Meek (1876, in caption to Pl. 37, fig. 4b), a left valve, L = 15.1, H = 17.1, $\frac{1}{2}$ W = 7.1, AL = 6.4 mm. Type locality: mouth of Judith River, Montana. Stratigraphic position: Judith River Formation, Campanian.

Hypotype YPM 24180 held at YPM.

MATERIAL AND OCCURRENCE. One articulated specimen and a left valve from two localities (88, 288) in the Timber Lake Member, one well-preserved fragmented left valve (YPM 24180) from Loc. 224, Bullhead lithofacies, and a left valve from Loc. 75, Hell Creek Formation.

Comparison. There are no obvious differences from type specimens of whitei. The Fox Hills specimens are, however, too incomplete to place with certainty in the species. Ethmocardium ursaniense Landes (1940) may be conspecific with whitei.

PROTOCARDIA

Type Species. By subsequent designation of Herrmannsen (1847, p. 336), Cardium hillanum Sowerby (1813, p. 41), Albian-Cenomanian, England.

Discussion. Meek (1876, p. 172–173) made *P. subquadrata* (Evans & Shumard) the type species of the subgenus *Leptocardia*. Dall (1900a, p. 1079) was doubtful of the significance of the morphological distinctions, size, thinness of the shell, general weakness of the radial costae and possession of two pallial sinuses, and considered that *Leptocardia* should be synonymized under *Protocardia* (see also Dall, 1900b, p. 385). Meek delimited two categories under *Leptocardia*, (a) "shells small, very thin about as long as high" as for *P. subquadrata*, and (b) "shells higher than long but very thin" as for *Cardium pertenue* Meek & Hayden (1861, p. 442). The validity of these sections is extremely doubtful especially if *pertenuis* is conspecific with *subquadrata* as suggested below. The variation of size, thickness of shell and of morphological features, notably for the point of appearance and strength of the costae, is large for *subquadrata*, and *Leptocardia* is here not accepted as a subgenus of *Protocardia*.

Many recent species have been included under *Protocardia*, but most workers (Meek; Tremlett, 1950; Stewart, 1930) consider that the genus did not survive into the Tertiary. Stewart (1930, p. 272) thought that the genus "disappeared before the close of the Cretaceous, perhaps during the Cenomanian". *P. subquadrata* extends into at least the uppermost Cretaceous (Maestrichtian) of the Western Interior. The species has not been recorded from the overlying marine Cannonball Formation (Paleocene; Stanton, 1920). Illustrations suggest that all the Recent species referred to *Protocardia* probably belong to *Nemocardium* (Keen, 1950) or closely related taxa.

Protocardia subquadrata (Evans & Shumard) (Plate 28, figs. 12, 13; Plate 29, figs. 1–16; Plate 30, figs. 1–3)

Cardium subquadratum Evans & Shumard, 1857, p. 39.

Cardium rarum Evans & Shumard, 1857, p. 39.

[?]Cardium pertenue Meek & Hayden, 1861, p. 442.

Cardium (Protocardia?) subquadratum Evans & Shumard. Meek, 1864a, p. 13.

Cardium (Protocardia?) rarum Evans & Shumard. Meek, 1864a, p. 12.

Protocardia (Leptocardia) subquadrata (Evans & Shumard). Meek, 1876, p. 175, Pl. 29, figs. 8a-e.

Protocardia (Leptocardia) rara (Evans & Shumard). Meek, 1876, p. 176, Pl. 17, figs. Ia-c.

[?]Protocardia (Leptocardia?) pertenuis (Meek & Hayden). Meek, 1876, p. 176, figs. 13, 14.

Protocardia subquadrata (Evans & Shumard). Kellum, 1962, p. 59, Pl. 2, fig. 13; Pl. 3, figs. 4, 7, 8.

[?]Protocardia? sp. Kellum, 1962, p. 60, Pl. 3, fig. 3.

Description. Specimens 1.8 to 24.8 mm long, inequilateral, equivalve, moderately inflated. Shape rather consistent, subtrapezoidal, the posterior margin truncated with the posterodorsal part convex to weakly concave, the anterior margin rounded. Height, anterior length and width, respectively, 81.0 to 100.0 (N = 314, μ = 92.3%), 33.6 to 49.4 (N = 314, μ = 43.6%) and 48.6 to 74.4 (N = 313, μ = 59.1%) percent of length. Escutcheon narrow, lanceolate, 13.5 to 35.6 (N = 202, μ = 22.0%) percent of length, each valve with a faint narrow sulcus, most prominent on left valve, external to margin of escutcheon (Pl. 29, fig. 4). Umbones moderately to strongly gibbose, incurved, prosogyrous. Ligament external, opisthodetic, parivincular, supported on nymphs.

Shell ornamented by fine concentric striae, bent ventrally and most distinct over costae, sometimes by irregularly spaced growth constrictions, and on posterior third by 12 to 23 slightly elevated, flat- to round-topped radial costae which are narrower than intervening depressions. Costae appear at 5 to 12 mm height, faint on many and absent on some specimens (Pl. 29, fig. 1). Posteroventral margin crenulated, the costae forming incurving, round-pointed projections, strongest immediately anterior to posteroventral angulation. Projections extend dorsally and anteriorly around shell margin for varying distances from angulation. Crenules present on smallest specimens, sometimes faint, rarely absent (Pl. 29, fig. 1).

Hinge line 56.5 to 65.7 (N = 21, μ = 61.9%) percent of length, arched, of variable massiveness, right valve hinge slightly longer. Anterodorsal margin continues posteriorly to form the roof of the posterior cardinal tooth cavity (Pl. 29, fig. 10). Heterodont, each valve with two cardinal teeth that show some variation in form and size, mostly conical, but some tend to be lamellar especially the smaller cardinal tooth. Anterior cardinal of right valve and posterior of left valve much smaller than the other, that on the right valve sometimes minute. Lateral teeth at extremities of hinge, well separated from cardinals. Right valve with two posterior and two anterior laterals, the ventral lamellar and two to three times longer than dorsal. The posterior dorsal lateral is an extension of dorsal margin to overlap the margin of the left valve (Pl. 29, fig. 5). Left valve with one anterior and one posterior lateral tooth, the posterior weak, lamellar, situated just below dorsal margin, the anterior strong, lamellar, below a socket for reception of dorsal anterior lateral of right valve. Nymphs strong, of variable shape, posterior end tapering (mostly) or truncated, the upper surface thins posteriorly, slopes toward commissure, marked by fine grooves and striae for insertion of ligament, length 23.1 to 33.3 (N = 21, μ = 27.3%) percent of length of hinge.

Adductor insertion area situated below end of lateral teeth, subequal, elongate-oval, the posterior slightly larger than anterior, impressed, especially along inner margin. Anterior pedal retractor insertion arched, impressed, linear, extends along base of ventral lateral tooth, continuous with adductor, its posterior end deeply impressed and bulbous, the anterior end sometimes wide and impressed tending to give the adductor a tear-drop shape (Pl. 29, fig. 15). Posterior pedal insertion discrete, that of right valve on ventral surface of ventral lateral tooth, narrow, elliptical, impressed; pedal insertion area of left valve impressed, elongate, along basal margin of socket for reception of ventral lateral tooth of right valve (Pl. 29, fig. 7). An oval, deeply impressed, pedal insertion is situated in the umbonal cavity behind the anterior cardinal tooth. Pallial line with one to three, rarely less than three, shallow, open indentations, the dorsal one under the adductor least definite and most often absent, the middle indentation most open, rarely absent (Pl. 29, fig. 7). Pallial line joins the center of ventral margin of anterior adductor and anteroventral extremity of posterior adductor

and anteroventral extremity of posterior adductor.

Ostracum thin, 0.05 to 0.5 mm thick on specimens 10 to 15 mm long, but 0.9 mm for a specimen 24.8 mm long, of three layers. An outer thick concentric cross-lamellar layer, a very thin myostracum and an inner thin complex cross-lamellar layer.

Types. The location of the holotype of subquadrata is unknown. Type locality: Moreau River. Stratigraphic position: almost certainly from the Fox Hills Formation. The location of the holotype of rarum is also unknown. Type locality: Moreau and Grand Rivers. Stratigraphic position: its recorded (Evans & Shumard, 1857) association with Limopsis striatopunctatus indicates derivation from Limopsis-Pseudoptera or Protocardia-Oxytoma assemblage zones, Fox Hills Formation.

Types held at YPM are: hypotypes YPM 24184-24200, 24376-77, 24477, 24649.

Discussion. Few specimens exceed 17 mm in length and only one (YPM 24198, L = 24.8 mm; Pl. 28, fig. 12) is longer than 20 mm. This large right valve has all the external morphological features characteristic of smaller specimens and is undoubtedly conspecific. Morphological variation is slight, exceptions being for the point of appearance and strength of the costae, a tendency for inflation to increase with size (Fig. 16) and the number of sinuses in the pallial line. On some specimens the costae become plicate below the pallial line. A faint sulcus is sometimes present dorsal to the rounded umbonal to posteroventral angulation. Shell damage resulting in growth distortions is common. The shell normally has a vitreous appearance except where eroded and pitted during life or subsequently weathered. A light-gray coloration is common, while the more general creamy or white appearance is probably due to different degrees and processes of weathering. Erosion and pitting of the umbone is common. This originated during the life cycle of the species as it does for recent species of Cardium (Johnstone, 1899).

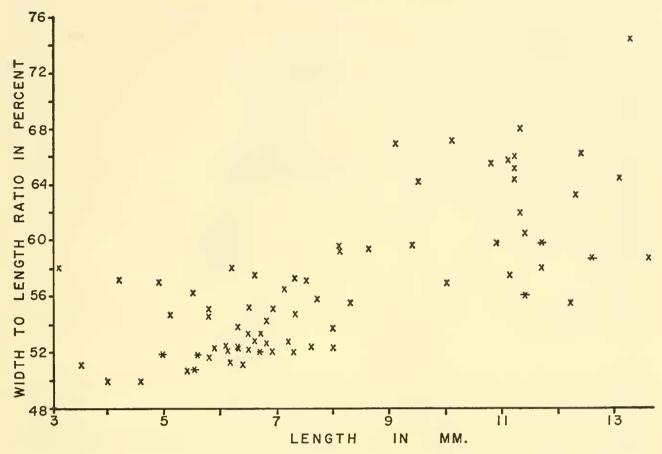


Fig. 16. Protocardia subquadrata. Scatter diagram of length plotted against width to length ratio (expressed as percentage), showing a tendency for greater inflation with increasing length (size). Loc. 92, A921, N = 82. * = >1 specimen.

Ligament material remains attached to the nymphs of many specimens, particularly in nonweathered samples. In a concretion (A921) from the *Cucullaea* Assemblage Zone, 61 of 78 articulated specimens possessed ligament material. The process of extraction probably removed the ligament of many of the remaining specimens. Samples from other assemblage zones in both the Trail City and Timber Lake members have a comparable high ratio. The ligament material consists of pearly fibrous inner layer of authors (Newell, 1937; Trueman, 1949). The form, dimensions and position of the ligament suggest that in most cases the outer lamellar layer has been removed. One specimen (YPM 24649) has traces of a dark material, perhaps the lamellar outer layer, as described for *Cardium corbis* Martyn by Mitchell (1935).

The adductor and pedal musculature is closely analogous to that of Cardium edule Linnaeus (Johnstone, 1899) and Corculum hemicardium (Linnaeus) (Pelseneer, 1911, Pl. 21, fig. 2). The linear anterior insertion area probably represents a fusion of the pedal protractor, the ventral part continuous with the adductor insertion area, and the pedal retractor the more deeply impressed posterodorsal part. A minor difference is that the anterior and posterior pedal insertions, especially the latter, are more intimately associated with the lateral teeth. The pallial line is very remote from the ventral margin of the valve, especially posteroventrally in the vicinity of the pallial indentations. This suggests that the prominent line taken as the pallial line might be due to other anatomical structures such as that produced by impression of the pallial blood vessel in Lucina (Allen, 1958). The consistency of the line, its connection and cessation at the adductor, and the occurrence of complex cross-lamellar shell layer inside the line and cross-lamellar outside, which conforms to the normal pattern of secretion of shell layers, indicate that the line marks the point of pallial attachment.

MATERIAL. Approximately 30,000 specimens as individuals and in selected blocks and concretions.

Occurrence. Protocardia subquadrata occurs in all major assemblage zones of the Trail City and Timber Lake members, and is also present in Iron Lightning Member. In the Trail City Member it is a dominant species only in the Protocardia-Oxytoma Assemblage Zone, although it also occurs as a codominant in scattered Discoscaphites-Protocardia associations in the Lower nicolleti Assemblage Zone. The species is particularly abundant in the marine biofacies of the Timber Lake Member and in the sequence to the northeast of Grand River where the Timber Lake sandstones descend in the section, and occurs as a dominant and codominant in all major assemblage zones.

Articulated valves dominate assemblages in which *Protocardia* is abundant. Exceptions occur in the Lower *nicolleti* Assemblage Zone, and especially in concretions in assemblage zones of the Timber Lake Member. Even in the latter, which were deposited in a more dynamic environment, the exceptions are subordinate. When single valves are numerous left and right valves are usually present in the same order of magnitude. *Protocardia*, like *Limopsis* (p. 47), also shows common restriction of a limited range of size classes to individual concretions and clustering of different size classes in concretions (Fig. 17).

Protocardia subquadrata is reported from many sections in the Upper Cretaceous of the Western Interior of the United States (Robinson and others, 1959; Griffitts, 1949)

and south-central Canada (Gleddie, 1949; Warren, 1934).

Comparisons. Evans and Shumard (1857) described but did not illustrate two species, subquadrata and rara, from the region of the Grand and Moreau Rivers. All the morphologic differences (size, shape, thin and polished shell, strength of costae, prominence of beaks and shape of posterior adductors) used by them and Meek (1876, p. 176) to distinguish the two species fall within the range of variation of assemblages from individ-

ual concretions. As subquadrata was described first the name has priority.

Protocardia pertenuis (Meek & Hayden, 1861) from Deer Creek, North Branch of Platte River, has similar general morphology. Meek distinguished it from subquadrata on the basis of the greater height than length measurement. The height to length ratio percentage of 110.2 percent and the width to length of 84.8 percent for the specimen figured by Meek (1876, p. 176) are greater than the maximum values (H/L = 100.0%, W/L = 74.4%) for subquadrata. As subquadrata shows an increase in inflation with increasing length (Fig. 16), the differences may not be significant. A decision whether the two species are conspecific should await a detailed study of an adequate number of specimens of pertenuis from the type locality.

Comparison with the original specimen (in collection USNM 298) shows that Meek

(1876, Pl. 29), made the pallial sinuses of figure 8e too large.

Protocardia sp. A (Plate 30, figs. 4-6)

Description. Large, specimens 53.8 to 63 mm long, equivalve, inequilateral. Umbones at about anterior third, strong, projecting 10 to 15 percent of height above dorsal margin, strongly incurved, prosogyrous. Strongly inflated, maximum inflation in dorsal third. Escutcheon long and narrow. Subquadrangular, about as long as high, anterior end narrower than posterior. Anterodorsal margin straight, meets rounded anterior end at an angulation, continuous with convex ventral margin. Posterior end truncated, the ventral angulation more distinct. Height, half width and anterior length for N = 6, respectively, 91.3 to 101.6 (μ = 96.5%), 31.4 to 36.7 (μ = 33.5%) and 32.0 to 37.2 (μ = 34.8%) percent of length. Twenty-six to 30 prominent, flat-topped costae on posterior third of shell, strongest anterior to the umbonal to posteroventral angulation. Costae end in strong incurving projections giving a crenulated posteroventral margin. Radial ornament crossed by fine concentric striae, growth ridges and depressions.

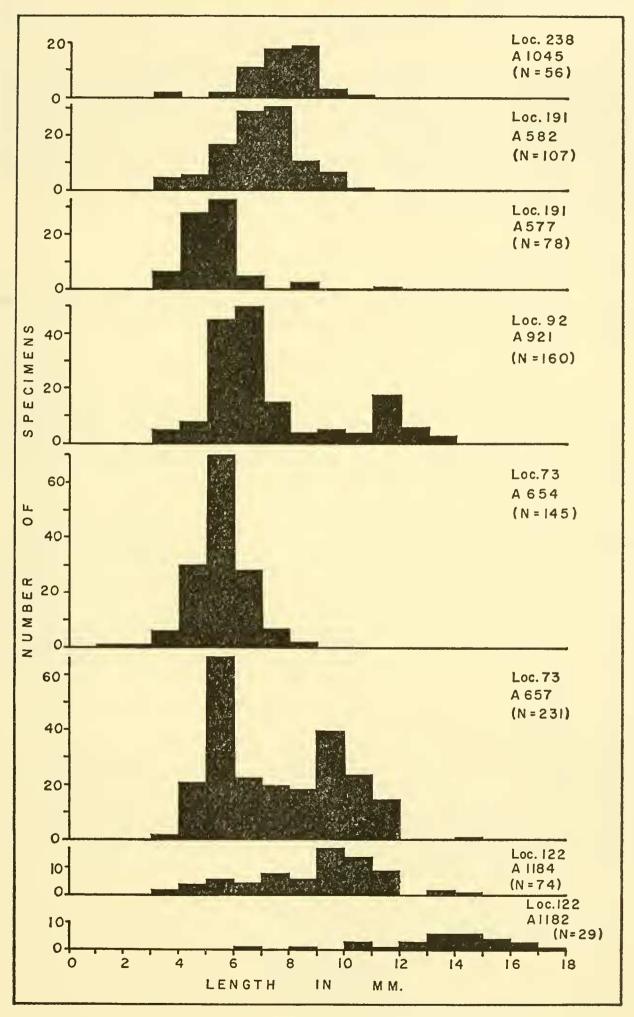


Fig. 17. Size-frequency histograms of Protocardia subquadrata from samples of concretions.

Hinge strong, occupies most of dorsal margin, dental formula

Lateral teeth at extremities of hinge, AIII small and elongated, the remainder long, strong and projecting. Lateral PI has a bulbous dorsal surface, fits under PII. Cardinal teeth 2b and 3b strong, triangular and projecting, 4b more lamellar but still strong and projecting, 3a small conical, weakly delimited from the dorsal margin. Ligament external, borne on short strong nymphs. Heteromyarian, muscle insertion areas situated below ends of hinge. Anterior adductor smaller, subquadrangular, the posterodorsal margin concave. Posterior adductor large, suboval. Pedal retractor insertions and umbonal insertion as described for subquadrata. Pallial line with a shallow ventrally situated sinus.

Ostracum up to 2.0 mm thick. Layering as for subquadrata.

Types. Hypotypes held by YPM are: YPM 24181-83.

Discussion. As the measurements were made on only six specimens extreme values are unlikely to have been obtained. Costae were counted on only two specimens.

MATERIAL. 17 specimens, mostly poorly preserved steinkerns.

Occurrence. This rare species occurs as single specimens and, rarely, two individuals per concretion. One concretion (A545) contained four individuals. One specimen came from the *Protocardia-Oxytoma* Assemblage Zone, the remainder from Lower *nicolleti* Assemblage Zone. The species is relatively common in the vicinity of Localities 216, 218 and 219, where 11 of the specimens were found.

Comparisons. Protocardia sp. A is three to four times longer than the average subquadrata, has more anteriorly situated and prominent umbones, a narrower anterior end and may have more costae. P. subquadrata has 23 or fewer costae compared to known minimum of 26 for P. sp. A. The two species occur together at all but one locality and as they are so similar in all other respects there seemed the possibility that the large specimens might be due to growth in a favored environment, as described by Kristensen (1957) for abnormally large individuals of Ensis. Against this is the very local geographic and stratigraphic distribution of P. sp. A. Difficult to explain is the discovery of only one specimen in assemblage zones where subquadrata is considerably more abundant compared with the Lower nicolleti Assemblage Zone. Because of the morphological and ecological differences P. sp. A is considered a valid species, although how its juveniles could be distinguished from subquadrata is problematical.

Whiteaves (1885) described *P. borealis* from the "Fox Hills" and "Fort Pierre Groups" (Upper Cretaceous) of the Bow and Belly rivers region, southern Alberta. Like *Protocardia* sp. A this species has prominent anteriorly situated umbones and a height to length ratio of about one. The average specimen is about 23 mm long, but a stein-kern, 41 mm long, from Ross Coulee was considered conspecific. Whiteaves recorded the association of *subquadrata* with *borealis*. His figures and measurements suggest that *borealis* might be conspecific with *Protocardia* sp. A. Hence no new name is at present given to the Fox Hills specimens.

VENERACEA

DOSINIOPSIS

Author. Conrad, 1864, p. 213.

Type Species. By subsequent designation of Tate (1868, p. 76), Dosiniopsis lenticularis meeki Conrad (1864, p. 213; see Tremlett, 1953, p. 7), Eocene, Maryland.

Discussion. Casey (1952) and Tremlett (1953) list and discuss the morphological characters distinguishing *Dosiniopsis* from closely related venerid genera. The fusion of AIII to 3a and the rugose band along the dorsal margin of the nymph are well developed on *D. deweyi* (Meck and Hayden). This species, contrary to the familial diagnosis of Casey, has the pedal scars fused to the adductors. On the basis of Casey's and Tremlett's studies many venerid species described from Upper Cretaceous sequences in the United States require reexamination to ascertain their generic affinities and relationships.

Dosiniopsis deweyi (Meek & Hayden) (Plate 31, figs. 1-19)

Cytherea deweyi Meek & Hayden, 1856a, p. 83.

Cytherea nebrascensis Meek & Hayden, 1856a, p. 83. [?]Cytherea owenana Meek & Hayden, 1856c, p. 273.

[?] Cytherea pellucida Meek & Hayden, 1856c, p. 272.

Meretrix deweyi (Meek & Hayden). Meek & Hayden, 1860a, p. 185.

[?] Meretrix owenana (Meek & Hayden). Meek & Hayden, 1860a, p. 185.

[?] Meretrix pellucida (Meek & Hayden). Meek & Hayden, 1860a, p. 185.

Callista deweyi (Meek & Hayden). Meek & Hayden, 1861, p. 443.

Callista deweyi var. robusta Meek & Hayden, 1861, p. 443. Meek, 1876, p. 184.

Dione deweyi (Meek & Hayden). Meek, 1864a, p. 13.

Dione nebrascensis (Meek & Hayden). Meek, 1864a, p. 13.

[?] Dione owenana (Meek & Hayden). Meek, 1864a, p. 13.

[?]Dione? pellucida (Meek & Hayden). Meek, 1864a, p. 13.

Callista (Dosiniopsis?) deweyi (Meek & Hayden). Meek, 1876, p. 182, Pl. 17, figs. 15a-e. Stanton, 1920, p. 31, Pl. 5, figs. 11, 12.

Callista (Dosiniopsis) nebrascensis (Meek & Hayden). Meek, 1876, p. 184, figs. 15-17. Stanton,

1920, p. 30, Pl. 5, figs. 5–10 (figs. 8a,b \equiv Meek's type).

[?] Callista (Dosiniopsis) owenana (Meek & Hayden). Meek, 1876, p. 183, Pl. 37, fig. 1. [?] Callista? pellucida (Meek & Hayden). Meek, 1876, p. 187, Pl. 17, figs. 10a-e, 12a-c.

[?]Dosinia missouriana? (Morton). Whitfield, 1880, p. 416, Pl. 11, figs. 25, 26.

Callista (Dosiniopsis) deweyi (Meek & Hayden). Whiteaves, 1885, p. 42, Pl. 6, figs. 4, 5, 5a.

Dosiniopsis nebrascensis (Meek & Hayden). Stewart, 1930, p. 252.

Calva nebrascensis (Meek & Hayden). Tentatively assigned by Popenoe, 1937, p. 395.

Trigonocallista deweyi (Meek & Hayden). Shimer & Shrock, 1944, p. 427.

Dosiniopsis deweyi (Meek & Hayden). Cvancara, 1966, p. 338, fig. 6; Pl. 7, figs. 2, 3; Pl. 8, figs. 13, 14, 16–18.

Description. Length of specimens 7.6 to 40.3 mm, equivalve, inequilateral, moderately inflated with maximum inflation in dorsal half, umbones moderately prominent, weakly prosogyrous. Lunule indefinite, delimited by shallow grooves. Escutcheon narrow, depressed, sunken, especially posteriorly. Shape suboval to suborbicular, the anterodorsal margin slightly concave, the posterodorsal and posterior margin rounded or generally weakly convex with an angulation at about half the height and a less distinct one ventrally with the margin between straight or convex. Ventral and anterior margins a continuous curve. Height, half inflation, anterior length and length of escutcheon, respectively, 84.5 to 96.5 (N = 90, μ = 90.6%), 18.8 to 29.1 (N = 90, μ = 24.3%), 31.6 to 43.6 (N = 90, μ = 38.4%) and 28.5 to 41.5 (N = 54, μ = 35%) percent of length. Shell ornamented with concentric striae and fine irregular costae and growth pause depressions. On some specimens the costae are more regular dorsally.

Hinge occupies most of dorsal margin, arched and elongated posteroventrally.

Dentition cyrenoid:

$$\frac{\text{AIII} \quad \text{AI} \quad 3\text{a} \quad \text{I} \quad 3\text{b} \quad \text{PI}}{\text{AII} \quad 2\text{a} \quad 2\text{b}_2 \quad 4\text{b} \quad \text{PII}} \ .$$

AI long, strong, elongated parallel to dorsal margin, with a grooved and ridged dorsal surface. AIII lamellar, strongly to weakly projecting, especially anteriorly, ventral surface sometimes grooved and ridged, continuous with 3a. The socket between the lateral teeth is continuous with the socket for 2a. AII strong, parallel to margin, serrated and ridged ventrally and sometimes dorsally, separated from 2a by a broad socket. Posterior laterals remote, grooves above continuous with ligament socket. PI smooth, of variable strength, more or less forms a continuous plate with nymph. PII weak. Anterior two cardinals in each valve are fused dorsally but are separate from dorsal margin, although 3a tends to be fused at mid-length if the dorsal margin is downfolded. Cardinal 3a lamellar, opisthoclinal, normally curved anteriorly; I close to 3a, orthoclinal, more massive and triangular, slightly concave anteriorly, beveled and ridged on posterior side, separated by a wide socket from a bifid 3b which is prosoclinal and continuous with anterior margin. Cusps of 3b lamellar and projecting. The tooth is separated from the nymph by a deep socket. Cardinal teeth of left valve more uniformly spaced. Cardinal 2a thin lamellar, opisthoclinal and concave anteriorly. Cardinal tooth 2b2 prosoclinal, trigonal, with a sharp projecting posterior edge that tends to be pointed ventrally, beveled and ridged on anterior side with a ridge at its base extending toward 2a, and a wide socket posteriorly that may have a ridge along its posteroventral margin. 4b long, lamellar, prosoclinal, separated from nymph by a shallow groove. Ligament external, on relatively strong and long nymphs which are narrow anteriorly and broad posteriorly, flat or concave dorsally, and widest anteriorly. Dorsal margin of nymph with a narrow rugose band, rugae weakest posteriorly, underlain by a sulcus of variable strength.

Heteromyarian; the anterior adductor insertion area tear-shaped and slightly smaller, but longer, than the posterior pear-shaped insertion. Posterior pedal retractor narrow, linear, continuous with adductor and extends under hinge to posterior end of nymph. Anterior pedal retractor subquadrangular, fused to adductor, under anterior end of lateral. A line of pallial attachment extends from anterior pedal insertion area to under posterior two cardinal teeth where there are two swellings. Two small linear insertion areas are situated below these on the posterior side of the umbonal cavity. Pallial line with a moderately deep triangular sinus, the apex pointing horizontally or postero-

dorsally.

Ostracum up to 1.4 mm thick, of two layers. A thin outer layer of short plates or prisms dipping at about 60 degrees to the surface, and an inner apparently homogeneous layer three to four times thicker.

Types. Lectotype of Cytherea deweyi Meek & Hayden, in collection USNM 341, here designated, a bivalved specimen lacking most shell on the right valve, L = 22.9, H = 20.9, W = 13.1, AL = 7.1 mm, figured by Meek (Pl. 17, fig. 15a,c) and labeled by him as type, as follows: "The specimen marked Mo is from Moreau River and is the type of this sp.; the others Y.S. are from Yellowstone River and may be distinct". Type locality: Moreau River, South Dakota. Stratigraphic position: Fox Hills Formation, probably from the Timber Lake Member. Lectotype of Cytherea nebrascensis Meek & Hayden, in collection USNM 323, labeled as type by Meek, but by subsequent designation of Stanton (1920, p. 30, Pl. 5, figs. 8a, b), a bivalved specimen with shell missing from the ventral margin, L = 17.6, H = 15.3, W = 7.1, AL = 7.4 mm. Type locality: Moreau River, South Dakota. Stratigraphic position: "Upper part of Pierre Shale", Maestrichtian. Lectotype of Cytherea owenana Meek & Hayden, USNM 176, by subsequent designation of Meek (1876, in caption to Pl. 37, fig. 1), a gaping steinkern with some shell, the right valve incomplete, L = 39.2, H = 34.6, 1/2 W = 5.2, AL = 15.2 mm. The pallial sinus on Meek's figure is directed more horizontally than indicated. Type locality: mouth of Judith River, Montana, Stratigraphic position: Judith River Formation, Campanian. Lectotype of Callista deweyi var. robusta Meek & Hayden, here designated, the original of figure 15 (Meek, 1876, p. 184), in collection USNM 1938, a bivalved shell with adhering matrix. The drawing is greatly idealized. Type locality: Deer Creek, North Platte River, Wyoming. Stratigraphic position: Fox Hills Formation, probably Maestrichtian. Meek later included the Deer Creek specimens in nebrascensis and based his revised description on them. Lectotype of Cytherea pellucida Meek & Hayden, in collection USNM 418, by subsequent designation of Meek (1876, in caption to P1. 17, fig. 10a; specimen also the original of figs. 10b, d) a two-valved specimen with some shell, L=21.9, H=19.1, W=10.4, AL=7.7 mm. Type locality: 200 miles above mouth of Milk River, Montana. Stratigraphic position: Judith River Formation, Campanian.

Types held at YPM are: hypotypes YPM 24169-71, 24173-79, 24708-11.

Discussion. Two samples from localities about three miles apart differ slightly in shape, their mean values for height to length and width to length ratios differing by 3.0 and 1.5 percent. A sample of 19 from Loc. 183 are lower and stouter than a sample of 38 from Loc. 83, the values being 88 and 25.6 compared to 92 and 24.2 percent respectively. Application of the Wilcoxon nonparametric test (Bradley, 1960) showed that these differences are not significant at the 95 percent level of probability and probably represent local phenotypic variation. Some specimens are compressed and very thin shelled. Specimens from most localities retain ligament material, consisting of an inner pearly fibrous layer and a thin brownish outer layer. The latter is sometimes continuous with a thin granular vitreous layer that is present on parts of the shell and which is perhaps the periostracum. The homogeneity of the outer shell layer varies, there being concentric lighter colored bands that readily weather to a honeycomb structure and other narrow resistant bands that project as raised ridges (P1. 31, fig. 4). As the structure is consistent the difference may be compositional and related to seasonal growth rates. If this is true large specimens lived for 12 to 14 years, not an excessive life for some bivalves. Yet the occurrence of finer bands between the larger indicates that other factors, possibly reproduction, were operative. The ease of erosion of the outer layer tends to destroy the detail of the ornamentation.

The hinge teeth are very consistent in shape and position, even on the smallest specimens available. The commissure in front of the umbone of a few specimens is slightly depressed and tends to fuse to 3a or, on the left valve, to develop a small projection on the side of the socket for 3a. The nymph and posterior end of the escutcheon are more variable. The rugose band may be weak, or a concave flange may project above the band from the outside edge of the nymph (P1. 31, fig. 18). Others (YPM 24175) have the escutcheon elongated, the posterior lateral suppressed, and the posterior end of the nymph tending to elongate and swell and to act as a lateral, and for the anterior end of the nymph to tilt strongly inward. Disease or physical damage may have caused these effects.

MATERIAL. 448 specimens as individuals and in concretions.

Occurrence. Ninety-five point five percent were collected from the basal part of the *Tancredia-Ophiomorpha* Biofacies, where it is the dominant element occurring in small shellbeds as single valves and articulated specimens scattered through the matrix and in small concretions dominated by articulated shells.

There are few records of *Dosiniopsis* species in the Upper Cretaceous of the Western Interior. D. deweyi, in addition to the references above, is recorded in the Fox Hills Formation (White, 1879a) and Pierre Shale (Griffitts, 1949) in the Rocky Ridge Sandstone Member in Colorado. These units are lithologically similar to the *Tancredia-Ophiomorpha* Biofacies. Hume (1926) recorded C. nebrascensis in the Ribstone Creek Formation, Alberta.

Comparisons. Meek and Hayden (1856a, p. 83) described two species, D. deweyi and nebrascensis, from beds at "Moreau River, No. 5 of the series". The geographic distribution of units mapped by Waage (1968) and the known occurrence of deweyi suggest that the specimens came from the Timber Lake Member, west of Route 63. D. nebrascensis was distinguished by its more compressed form. Meek's (1876) later description implied that deweyi had more regular concentric ornamentation. His mea-

surements, confirmed by reexamination of type specimens in USNM, fall within the range of values of samples from the type Fox Hills and, because of probable phenotypic variation, the "species" are considered conspecific. Meek's (1876) transference of his robusta from a variety of deweyi to nebrascensis indicates that he had difficulty in placing specimens. Dosiniopsis owenana and pellucida have almost identical height to length and width to length percentages, and the thicker shell and deeper sinus supposedly characteristic of owenana are not of species rank. The height to length ratio for Callista? pellucida, as originally quoted by Meek and Hayden (1856c), is 1.5 percent lower than any recorded by the writer. His (1876) later measurements fall within the range of deweyi. The thin shell of pellucida is not diagnostic. Meek (1876, p. 187) reports the occurrence of specimens of pellucida which are higher than long, but these were not found in his collection (USNM 418). Some do have a greater height to length ratio than recorded for deweyi.

Most of the species of *Dosiniopsis* discussed were based on specimens which are extreme in one or more parameter. For example, *D. pellucida* includes specimens with greater height to length percentages than any other species and *D. nebrascensis* tends to be more compressed, especially specimens from the finer grained sediments of the Pierre Shale. While synonymy of the species is suggested by the sample measurement data presented in Table 4, biometric analysis of adequate fossil populations of species from units other than *Tancredia-Ophiomorpha* Biofacies, Fox Hills Formation are required to define their statistical limits and status.

MACTRACEA

SPISULA

Аитнов. Gray, 1837, р. 372.

Type Species. By subsequent designation of Gray (1847, p. 185), Cardium solidum Linnaeus (1758, p. 681), Recent, Europe.

Spisula? sp. indet. (Plate 32, figs. 1-3)

Two crushed and incomplete specimens from Loc. 93, two crushed specimens from Loc. 74 and 10 hinge fragments and three incomplete valves from Loc. 224, all in the Bullhead lithofacies, are attributed to this species. Scattered incomplete specimens were also found in Colgate lithofacies, Iron Lightning Member.

Largest valve about 35 mm long, elongate-subtrigonal, shell thin with fine concentric striae which are strongest on the anterodorsal flank. Hinge relatively massive, laterals and cardinals close together. Dental formula:

AIII AI 3a 3b PI PIII
AII 2a 2b PII

Laterals small, prominent, projecting, the dorsal laterals of the right valve weaker than the ventral, the socket between and the upper surface of AII and PII finely rugose. 3a thin lamellar, approximately parallel to dorsal margin and ceases at end of socket for AII; 3b long lamellar, slightly opisthoclinal, convex anteriorly, fused to 3a and the dorsal margin. Cardinals of left valve Λ -shaped, the arms thin, lamellar, fused to dorsal margin. Chondrophore relatively large, shallow, margins raised, curving to point anteriorly. Dorsal margin below umbones with a prominent triangular notch, the anterior extremity on the commissure pointed and thickened as for *Cymbophora warrenana*.

Table 4. Ratios of H/L, W/L and AL/L, expressed as percentages, for small collections and lectotypes of "species" of Dosiniopsis. The underlined value is the mean.

		, A A	7			
	Name	Collection	Z	H/L%	W/L%	AL/L%
Η.	1. Cytherea deweyi	Fox Hills‡	06	84.5 - 90.6 - 96.5	37.6 - 48.6 - 58.1	31.6 - 36.4 - 43.6
2.	2. Cytherea deweyi	lectotype		91.3	57.2	31.0
3,	3. Cytherea deweyi	USNM 341	9	85.4 - 88.9 - 94.8	48.2 - 54.0 - 58.3	29.9 - 35.4 - 38.2
4.	4. Callista (D.) deweyi	USNM 32418* Stanton, 1920	2	85.6 and 92.5	50.4 and 55.0	40.2 and 43.0
5.	5. Cytherea nebrascensis	lectotype		86.9	40.3	42.0
9	6. Callista (D.) nebrascensis	USNM 32415* Stanton, 1920	3	90.4 - 91.7 - 93.4	43.7 - 46.1 - 48.5	34.2 - 35.6 - 36.6
7.	7. C. deweyi var. robusta	USNM 1938	∞	88.5 - 91.0 - 94.3	43.5 - 49.0 - 57.9	32.4 - 36.5 - 45.0
∞ _i	8. Cytherea owenana	lectotype		88.3	41.8	38.8
6	9. Dosinia missouriana	USNM 12249 Whitfield, 1880		89.0	53.8	32.4
10.	10. Cytherea pellucida	lectotype		87.2	41.5	35.2
11.	11. Cytherea pellucida	USNM 418	9	87.2 - 92.2 - 98.9	41.5 - 51.7 - 57.4	32.4 - 36 - 39.2

* From Cannonball Formation, Paleocene † From Tancredia-Ophiomorpha Biofacies

Outer ligament occupies a shallow groove along posterior limb of notch, not separated from chondrophore by a projection, and also apparently extends anteriorly for a short distance.

The gross arrangement of teeth resembles that of Mactrotoma fragilis (Gmelin), but the hinge details prove the relationship with Spisula sensu lato.

Types. Types held at YPM are: hypotypes YPM 24438-39.

CYMBOPHORA

Аитнов. Gabb, 1869, р. 180.

Type Species. By monotypy, Mactra ashburnerii Gabb (1864, p. 153, Pl. 22, fig. 127; 1869, p. 181, Pl. 29, fig. 69; Popenoe, 1937, Pl. 49, fig. 1), Chico Group, Upper Cretaceous, California.

Discussion. Although workers following Gabb made Cymbophora a subgenus of Mactra (Meek, 1876) or Spisula (Dall, 1898), more recent authors (Stewart, 1930; Popenoe, 1937; Stephenson, 1952) have been unanimous for generic status. The hinge of C. warrenana (Meek and Hayden) supports generic status, as differences from Mactra and Spisula include a large weakly bifid 2, a long lamellar 3b, both of which cross the height of the hinge, and a massive raised chondrophore with a very strong projecting posterior margin. The absence of a shelf between the chondrophore and the external ligament, and the rugose lateral teeth suggest a relationship with Spisula.

Cymbophora warrenana (Meek & Hayden) (Plate 32, figs. 4–19)

Mactra warrenana Meek & Hayden, 1856c, p. 271.

[?] Mactra formosa Meek & Hayden, 1856c, p. 271.

[?]Mactra alta Meek & Hayden, 1856c, p. 271.

[?] Mactra gracilis Meek & Hayden, 1860a, p. 179.

Mactra (Trigonella?) warrenana Meek & Hayden. Meek & Hayden, 1860b, p. 425.

[?] Mactra (Trigonella?) alta Meek & Hayden. Meek & Hayden, 1860b, p. 425.

[?] Mactra (Trigonella?) formosa Meek & Hayden. Meek & Hayden, 1860b, p. 425.

[?] Mactra (Trigonella?) gracilis Meek & Hayden. Meek & Hayden, 1860b, p. 425.

Mactra (Cymbophora?) warrenana Meek & Hayden. Meek, 1876, p. 208, Pl. 30, figs. 7a-d.

[?] Mactra (Cymbophora?) formosa Meek & Hayden. Meek, 1876, p. 207, Pl. 39, fig. 7.

[?]Mactra (Cymbophora?) alta Meek & Hayden. Meek, 1876, p. 210, Pl. 37, figs. 2a,b.

[?]Mactra (Cymbophora?) gracilis Meek & Hayden. Meek, 1876, p. 209, Pl. 17, figs. 18a, b.

[?] Mactra maia Whitfield, 1877, p. 144.

[?] Mactra (Cymbophora?) warrenana Meek & Hayden. Whiteaves, 1879, p. 142, Pl. 17, fig. 9; Pl. 19, figs. 3, 3a.

Mactra (Cymbophora) warrenana Meek & Hayden. Whiteaves, 1885, p. 43. [?] Mactra (Cymbophora) gracilis Meek & Hayden. Whiteaves, 1885, p. 43.

Description. Specimens 3.3 to 46.2 mm long, equivalve, inequilateral, maximum inflation in dorsal third, no lunule or escutcheon, umbones prominent and prosogyrous. Shape subtrigonal, the height, half width and anterior length, respectively, 75.3 to 87.8 (N = 60, $\mu = 81.5\%$), 20.5 to 31.1 (N = 60, $\mu = 25.8\%$) and 32.7 to 45.8 (N = 60, $\mu = 37.1\%$) percent of length. Shell with a sharp umbonal to posteroventral angulation, a weak umbonal to posterodorsal angulation and a weak umbonal to anteroventral angulation. These produce a marked posterior and a weak anterior truncation. Anterior angulation capped by a fine round-topped costa forms the ventral limit of a weak sulcus.

Posteroventral angulation irregular and raised where crossed by concentric ornament, forms the dorsal margin of a weak to strong broad shallow sulcus. Anterior end broadly or narrowly rounded depending on the height to length ratio, anterodorsal margin convex, posterodorsal margin straight or weakly convex, ventral margin broadly rounded. Ornament of fine concentric striae, growth ridges and depressions, and rare traces of broad flat-topped costae. Striae more prominent, closely spaced, and sharp crested across dorsal to ventral angulations, especially anteriorly. Ornament more regular and stronger on specimens less than 10 mm long.

Hinge long, arched; dental formula:

Laterals remote from cardinals, strong, AIII and PIII weaker than AI and PI. Sides of anterior and posterior sockets of right valve and upper surface of AII and PII rugose. Cardinal teeth displaced anteriorly by chondrophore; 3a strongly opisthoclinal, thin lamellar, convex dorsally, very projecting, and separated from a long thin prosoclinal 3b, the dorsal half of which forms the anterior wall of the chondrophore and is continuous with a thickened projection at the posterior end of the anterior margin. Cardinal tooth (2) of left valve large, strong, triangular, extends the height of the hinge, weakly bifid, separated from the thin lamellar anterior wall of the chondrophore by a narrow socket. Chondrophore large, prosoclinal, deeply concave and raised above surface of hinge plate, posterior wall thick with a broad flat striated top that may have acted as a sunken nymph. Dorsal margin of shell below umbone with a prominent triangular notch (Pl. 32, fig. 16). The outer ligament is inserted in a weak concavity along anterior limb of notch, not defined ventrally by a raised costa (Pl. 32, fig. 10).

Adductor insertion areas equal, their bases at about one third of height, continuous with the narrow elongated impression of the pallial line extensions (Owen, 1958) which extend under the lateral teeth. A series of small linear pits crosses the crest of the umbonal cavity and continues to near the anterior lateral where there is a larger oval insertion. Pallial sinus relatively short, narrow, the apex rounded. Posteroventral end of pallial line thickened. Ventral curved limb of pallial line broad, its dorsal surface irregular with flat-topped projections, sometimes with discrete knobs above. With growth these projections leave traces of faint flat-topped costae on the ventral part of the inner shell surface.

Ostracum relatively thin, up to 1.5 mm thick, of two layers. A very thick outer concentric cross-lamellar layer and a thin inner complex cross-lamellar layer. Either layer may have locally the structure of the other.

Types. Lectotype of Mactra warrenana Meek & Hayden, USNM 304, by subsequent designation of Meek (1876, in caption to Pl. 30, fig. 7a). The reportedly perfect type specimen was not located in collection USNM 304. Type locality: The original label with the collection reads "Cretaceous No. 5, Yankton Trading Post, Dakota", and the specimen may have come from the Long Lake locality. Stratigraphic position: Fox Hills Formation. Lectotype of Mactra formosa Meek & Hayden, USNM 177, here designated, the original of Plate 30, figure 7 of Meek (1876; labeled as type), a right valve, L=43.1, H = 33.7, $\frac{1}{2}$ W = 9.8, AL = 15.3 mm. Type locality: near mouth of Judith River, Montana. Stratigraphic position: Judith River Formation, Campanian. Lectotype of Mactra gracilis Meek & Hayden, USNM 297, by subsequent designation of Meek (1876, in caption to Pl. 17, fig. 18a), a small left valve with a damaged posteroventral margin, L = 12.5, H = 9.8, $\frac{1}{2}$ W = 2.4, AL = 5.3 mm. Type locality: Yellowstone River, near Miles City. Stratigraphic position: possibly from the Judith River Formation, Campanian. Lectotype of Mactra alta Meek & Hayden, USNM 192, by subsequent designation of Meek (1876, in caption to Pl. 37, fig. 2b), an incomplete right valve slightly compressed by compaction, L = 53.8, H = 48.4, $\frac{1}{2}$ W = c.13.0, AL = 19.4 mm. Type locality: Mouth of Judith River, Montana. Stratigraphic position: Judith River Formation, Campanian. Types held at YPM are: hypotypes YPM 24440-51.

Discussion. Small specimens tend to be higher, stouter and to have more medially situated umbones (Pl. 32, fig. 18). The pallial line of recent species of the genera Mactra, Spisula and Schizotherus is often broad and frequently corrugated along the dorsal margin. None have the strong projections of C. warrenana which, although more distinct and discrete from the main mass of the pallial line posteriorly, continue almost to the anterior adductor. These projections may be due to the need for a stronger pattern of musculation necessary for the formation of a waste canal by ventral mantle folds such as is present in many mactrids as an adaptation to aid life in silty water (Kellogg, 1915; Yonge, 1948). An anomaly is that the ventral mantle fold of recent species ceases before the pedal gape of the mantle. Although not distinct, as in many mactrids, the pedal retractor muscles are probably fused with the dorsal end of the adductor scars.

MATERIAL. 238 specimens, as individuals and in concretions.

Occurrence. The species is virtually restricted to the Cymbophora-Tellinimera Assemblage Zone (40.7%), to the northeastern part of Cucullaea Assemblage Zone (52.2%), Timber Lake Member, and their extensions into the Irish Creek lithofacies. It occurs as a dominant or codominant with Tellinimera and Protocardia. Single specimens are rare. One specimen came from Locality 83, Tancredia-Ophiomorpha Biofacies, and four from a medium-grained graywacke bed at Loc. 224, Bullhead lithofacies.

Comparisons. Meek and Hayden (1856c) named three species, Mactra formosa, warrenana and alta, in that order, on the same page. Later (1860b) they described a fourth species, M. gracilis, and Whitfield (1876) added a further species, M. maia. Meek (1876) thought that formosa, based on specimens from the mouth of Judith River, might be identical with warrenana. He also compared gracilis, from Yellowstone River, with warrenana, and alta with formosa. The last two species, and M. maia Whitfield, all come from near the mouth of the Judith River. The type specimen of alta has a high height to length percentage (90%) and, like associated specimens, is larger than any from the type area of the Fox Hills Formation. Compaction distortion has emphasized the umbone of the holotype. Other specimens in the collection have height to length percentages down to 80 percent, which is below the average (81.5%) for warrenana. M. gracilis was based on a juvenile specimen which can be matched perfectly by individuals from the Fox Hills collections. Measurements of type specimens of C. formosa, alta and gracilis held at the USNM, Washington fall within the range of variation of the total sample of C. warrenana from the Cucullaea and Cymbophora-Tellinimera assemblage zones, Timber Lake Member, Fox Hills Formation. However, biometric studies on adequate fossil populations of all species are required before their status is ascertained.

Whiteaves compared his specimens of M. warrenana from Vancouver and adjacent islands against specimens from the Western Interior sent by Meek and considered them identical. This should be checked.

Cymbophora? nitidula (Meek & Hayden) (Plate 33, fig. 1)

Tellina nitidula Meek & Hayden, 1861, p. 443. Mactra (Cymbophora?) nitidula (Meek & Hayden). Meek, 1876, p. 211, Pl. 30, figs. 6a-c.

Description. One small, incomplete, two-valved displaced specimen (YPM 24437) from Loc. 210 (A457), Cymbophora-Tellinimera Assemblage Zone, Timber Lake Member is classed here.

Elliptical, compressed, length approximately 12.0 mm, and half width 13.3 percent of length. Umbones moderately prominent and projecting, situated anterior of center. Posterodorsal margin immediately behind beaks tends to be auriculate. No lunule, but

a weak ridge, strongest near umbones, defines a posterodorsal area. Shell ornamented by fine irregular striae, growth depressions and ridges, strongest above the umbonal to posteroventral angulation. The latter is capped by a narrow raised welt. The right valve has a prominent triangular posterior lateral tooth. Other internal features unknown.

Types. Lectotype of *Tellina nitidula* Meek & Hayden, USNM 1913, by subsequent designation of Meek (1876, in caption to Pl. 30, fig. 6a), a right valve, L=24.2, H=18.2, 1/2 W=4.3, AL=9.7 mm. Type locality: Deer Creek, North Platte River, Wyoming. Stratigraphic position: Fox Hills Formation, probably Maestrichtian.

Hypotype YPM 24437 is held at YPM.

Discussion. Examination of the lectotype and topotypes indicates that *nitidula* is a valid species. The hinge, exposed by polishing by Meek (1876, p. 211–212), favors classification in *Cymbophora*.

TELLINACEA

PROTODONAX

Author. Vokes, 1945a, p. 295.

Type Species. By original designation (p. 295), Protodonax elongatus Vokes (1945a, p. 298), Colorado Group, Upper Cretaceous (Turonian-Conacian), Wyoming.

Protodonax? sp. indet. (Plate 33, fig. 2)

The Crassostrea bed at Loc. 97, Colgate lithofacies, yielded the anterior half of a left valve (YPM 24473) tentatively classed in Protodonax. The valve is donaciform, has a prominent prosogyrous almost terminal umbone, a concave, posterodorsal margin, a sharp strong umbonal to anteroventral angulation and weak concentric striae. It somewhat resembles P. umbonianus Vokes.

TELLINIMERA

Author. Conrad, 1860, p. 278.

Type Species. By subsequent designation of Conrad (1870, p. 73), Tellina (Tellinimera) eborea Conrad (1860, p. 278, Pl. 46, fig. 4), geographic and stratigraphic position uncertain (Stephenson, 1955, p. 122), possibly Upper Cretaceous of Mississippi.

Emended Diagnosis. Compressed subrectangular, umbones central or posterior of center, posteroventral margin reflexed laterally toward the right valve. Nymph moderately strong, projects prominently above the posterodorsal margin. Hinge long and narrow, two cardinal and lateral teeth in each valve, the cardinals close together and situated just posterior to umbones. Posterior cardinal of right valve and anterior of left valve strong, trigonal and made bifid by a narrow moderately deep notch. Anterior cardinal of right valve and posterior of left valve thin lamellar, especially the latter which is separated from nymph by a shallow groove and is fused to top of the anterior cardinal. One

posterior lateral on each valve, short distinct to weak protuberances, that on the right valve the stronger and with a small socket above. One anterior lateral on each valve, close to cardinals, small, right valve lateral the stronger and fits behind that of the left valve which is continuous with the dorsal margin. Anterodorsal margin of right valve has a shallow furrow which receives an interlocking linear protuberance on the left valve. Pallial sinus short and free (known only for *T. scitula* (Meek and Hayden), see below).

Discussion. Conrad (1860) proposed Tellinimera as a subgenus of Tellina and included two species, eborea and limatula, both from the Upper Cretaceous of Alabama and Mississippi. He later (1870) gave the taxon generic status, named eborea type, and illegally shortened the name to Tellimera. These early descriptions were quite inadequate (Stoliczka, 1870, p. 118; Stephenson, 1955, p. 122) and because of the partial dependence of modern tellinid systematics on internal morphology the name has been little used.

Although the internal morphology of the lectotype, ANSP 18769, is unknown, the external morphology indicates that it is probably congeneric with a specimen (USNM 131711) placed in *eborea* by Gardner (1916, p. 695, Pl. 42, figs. 5, 6), *Tellina buboana* Stephenson (1955, p. 121, Pl. 20, fig. 13; USNM 128161), Owl Creek Formation, Missouri, and the Western Interior species *T. scitula* (Meek & Hayden). The right valve of Gardner's two-valved displaced specimen of *eborea* shows the cardinal teeth and anterior part of the hinge. Like the hinge of *buboana* it differs only in minor detail from the hinge of *scitula*. Conrad (1870, p. 73) described the dentition of the left valve and not the right.

Tellinimera is distinguished from other tellinid genera by a combination of its compressed shape, projection of the nymph, dentition, and the short free pallial sinus which is fused to the pallial line for only a short distance posteroventrally. Externally it closely resembles Moerella Fischer (1887), but this genus and the similar Eurytellina Fischer (1887) have a deep sinus which may reach the anterior adductor muscle and is fused for most of its length. Other genera, Arcopagia, Apolymetis, Phylloda, etc., with a free pallial sinus are distinguished by their shape and hinge details.

Tellinimera scitula (Meek & Hayden) (Plate 33, figs. 3-15)

Tellina scitula Meek & Hayden, 1856a, p. 82.

Tellina? formosa Meek & Hayden, 1860a, p. 179.

Abra? formosa (Meek & Hayden). Meek, 1864a, p. 14.

Tellina (Peronaea? scitula Meek & Hayden. Meek, 1876, p. 197, Pl. 30, figs. 1a,b.

Linearia? formosa (Meek & Hayden). Meek, 1876, p. 199, Pl. 30, fig. 2.

Description. Specimens 6.0 to 26.8 mm long, equivalve, inequilateral, umbones just behind center, not projecting, strongly opisthogyrous. No lunule, and escutcheon virtually filled by nymph. Shape rather consistent, compressed elongate-subquadrangular, like Moerella Fischer, greatest height at and anterior to umbones, anterodorsal margin convex, anterior end rounded, posterodorsal margin slightly concave with a slight angulation posterior to escutcheon, posteroventral margin truncated. Ventral margin convex with a slight sinus anterior to the posteroventral extremity at the end of a broad shallow furrow extending from umbone to margin. Furrow most distinct on ventral half of shell, below a moderately sharp umbonal to posteroventral angulation which is most prominent dorsally. Posterior end weakly reflexed toward right valve. Height, half width, anterior length and length of nymph, respectively, 51.1 to 62.4 (N = 95, μ = 57.1%), 5.3 to 11.0 (N = 93, μ = 7.8%), 50 to 61.4 (N = 95, μ = 54.4%) and 10.5 to 19.9 (N = 42, μ = 14.8%) percent of length. Shell ornamented with fine concentric growth striae, lamellae and impressed lines, more prominent and closer together ventrally, weak on anterodorsal surface but closely spaced, strong and projecting as sharp narrow costae on posterior flank

above umbonal to posteroventral extremity ridge. Concentric ornament crossed by faint frequently discontinuous radial striae, strongest on anterior half of shell and visible only under certain lighting.

Hinge as described under diagnosis. Lateral teeth, especially the posterior, very weak. Ligament external, borne on moderately long strongly projecting nymphs the inner sur-

face of which forms a broad smooth plate between cardinals and posterior laterals.

Adductor insertion areas subequal, moderately impressed, situated under ends of hinge. Posterior adductor suboval, attenuated dorsally and continuous with a short subquadrangular pedal retractor insertion, from the end of which a linear impression extends to under lateral tooth. Anterior adductor longer, subquadrangular, its posterior margin irregular, weakly fused to or joined to the anterior pedal insertion by a narrow pallial impression. Anterior pedal insertion area L-shaped, consisting of a larger dorsal arm and a shorter arm extending ventrally from its posterior end. A linear pallial impression extends from pedal insertion to behind umbone, becomes discontinuous posteriorly. A small impressed oval insertion lies below anterior lateral, and several small pits occur in crest of umbonal cavity. Pallial sinus narrow, extends about half the length of the shell, its dorsal limb horizontal or slightly inclined dorsally, the apex narrowly or broadly rounded, and the ventral limb confluent with pallial line for posterior two to four millimeters. Posterior end of confluent portion bends downward. A weak linear impression joins posteroventral margin of adductor to dorsal extremity of pallial sinus.

Ostracum very thin, up to 0.5 mm thick. Structure complex cross-lamellar throughout with some homogeneous or prismatic layers locally in outer quarter or fifth of thickness. Inner surface of shell in umbonal cavity with strong vermiculated markings, and rounded ridges extend from dorsal ends of adductor scars toward umbonal cavity. Faint

radial striae are present below the pallial line.

Types. Lectotype of *Tellina scitula* Meek & Hayden, USNM 439, by subsequent designation of Meek (1876, in caption to Pl. 30, fig. 1a), a bivalved gaping shell, L=22.6, H=12.7, 1/2 W=1.4, AL=11.2 mm. Type locality: Moreau River, South Dakota. Stratigraphic position: Fox Hills Formation. The lithology and associated fossils indicate that the lectotype was collected from the Timber Lake Member. Lectotype of *Tellina? formosa* Meek & Hayden, USNM 396, by subsequent designation of Meek (1876, in caption to Pl. 30, fig. 2), a right valve shell, L=17.3, H=10.4, AL=8.0 mm. Type locality: 20 miles below the Cannonball River, on the Missouri, North Dakota. Stratigraphic position: Fox Hills Formation, from the Timber Lake Member.

Types held at YPM are: hypotypes YPM 24452, 24454-56, 24458-61, 24501; and

24453, 24457.

Discussion. Small specimens have relatively more prominent and posteriorly situated umbones. On many individuals the margin above the anterior lateral of the right valve is slightly thickened to simulate a lateral. Ligament material, consisting of a dark thin outer layer and a thick fibrous pearly inner layer, is preserved on numerous specimens. A cardinal ligament extends for a short distance anterior to the umbones (Trueman, 1949, fig. 1). The crest of the anterior lateral tooth of one right valve (YPM 24456) is crossed by small plaits.

MATERIAL. The description is based on 387 specimens. Three hundred and thirty-four more are held in collections.

Occurrence. Tellinimera scitula was collected from all assemblage zones of the Trail City and Timber Lake members and from one locality in the Bullhead Member. It is most numerous in the Timber Lake Member where it is characteristic of the Cymbophora-Tellinimera Assemblage Zone (27.2%) and is also common in the Cucullaea Assemblage Zone (20%). In these units the species occurs as a dominant or as a codominant with Cymbophora, Protocardia, and rarely with Ostrea translucida. T. scitula is wide-

spread and common only in Lower *nicolleti* Assemblage Zone (26.4%) of the Trail City Member, where it never occurs as a dominant. Articulated specimens dominate in nearly all concretions. A small proportion are bored.

There are few records of scitula other than those given by Meek (1876). White (1879a) recorded it from Upper Cretaceous sandstones in Colorado, and Kellum (1962)

from the Fox Hills Formation, Niobrara County, Wyoming.

Comparisons. Valid comparisons with other species are impossible until their internal morphology is well known. Tellina modesta Meek (1877, p. 157, Pl. 15, fig. 5; USNM 7852), Wasatch Ranges, is poorly preserved and probably specifically indeterminable, as is Stanton's (1893, p. 111, Pl. 25, fig. 3; USNM 22892) specimen from Coalville, Utah. The two specimens have lower height to length percentages than scitula. The lectotype (USNM 396; L = 17.3, H = 10.4 and AL = 8.0 mm) of Linearia? formosa is indistinguishable from scitula even to the possession of faint radial striae which led Meek (1876) to place it tentatively under Linearia.

SOURIMIS, new genus

ETYMOLOGY. Anagram of Missouri, gender masculine.

Type Species. Here designated, Tellina equilateralis Meek & Hayden (1856a, p. 82), Upper Cretaceous (Maestrichtian), Western Interior, U.S.A.

Diagnosis. Elongate elliptical, compressed, inequilateral, equivalve, posteroventral extremity twisted to the left, delimited by a weak sulcus on the right valve and a weak keel on the left valve. Anterodorsal margin downflexed to form a shallow lanceolate lunular area. The posterodorsal surface is flat (Pl. 34, fig. 6). Ornament variable, of weak concentric striae and threads, or growth depressions and ridges. Ligament external on long strong nymphs. Hinge relatively massive, extending about three quarters the length of the dorsal margin. Dental formula:

Cardinal teeth relatively strong and projecting; 3a lamellar, vertical or slightly opisthoclinal, separated by a narrow very deep linear socket from a similar but stronger 3b which is differentiated from the dorsal part of the nymph by a small notch. 2 narrow lamellar, very projecting, vertical or weakly opisthoclinal, separated from the nymph by a prominent socket. Sockets for 3a and 3b covered by the dorsal margin which tends to simulate teeth. Laterals remote; posterior separated from cardinals by featureless surface of the long nymph. Anterior laterals stronger than posterior, especially that of the right valve, and posterior ventral lateral of right valve longer and stronger than the two short left valve posterior laterals. AII fits above AI. PII is the thickened dorsal margin, and the anterodorsal margin of the right valve also sometimes tends to simulate a lateral tooth.

Adductor insertion areas situated under and behind lateral teeth, unequal, impressed, the anterior more so than the posterior. Anterior adductor smaller, subquadrangular, tapering dorsally. Posterior adductor stout pear-shaped, tapering dorsally. A narrow deeply impressed insertion area occurs under the hinge in front of the anterior cardinal. The posterior margin of the anterior adductor is buttressed by a strong ridge extending from under the cardinal teeth. A small weak ridge extends from near umbone to anterior margin of posterior adductor. Pallial line remote from margin, sinus deep extending one half to two thirds of the length, its apex narrowly rounded, dorsal limb horizontal, the posteroventral end twists slightly downward, not fused to ventral part of pallial line.

Discussion. The hinge structure and pallial sinus of *Sourimis* resembles those of species of *Arcopagia* which, however, are distinguished by the presence of two cardinal teeth in each valve, the right posterior and the left anterior generally being bifid, by the proximity of anterior laterals to the cardinals, the presence of one weak or no laterals on the left valve, and the possession of more sunken nymphs. *Arcopagia crassa* (Pennant), the type species, has a small impressed lunule. The dentition of *Solyma* Conrad (1870; Stephenson, 1952), classed in the Tellinidae, is similar to that of *Sourimis* but it lacks laterals, the cardinals are more massive and opisthoclinal, and 3b is separated from the nymph by a distinct socket. There is a close relationship between the two genera.

In general shape and dentition Sourimis resembles Corbicella Cox (1929), a member of the Tancrediidae. However, Corbicella has more prominent umbones, the pallial sinus is weak or absent, and there are many minor hinge differences. Its nymph is shorter, the anterior laterals are less distinct or absent, the posterior laterals are closer to the cardinals and there are two on the right valve and one on the left valve, and the left

posterior and the right anterior cardinals are weak.

Because of the deep sinus, the posteroventral flexure and the gross resemblance of the hinge to that of *Arcopagia*, *Sourimis* is placed in the family Tellinidae.

Sourimis equilateralis (Meek & Hayden) (Plate 34, figs. 1–10)

Tellina equilateralis Meek & Hayden, 1856a, p. 82. White, 1879a, p. 183. [?] Landes, 1940, p. 157. Tellina (Peronaea?) equilateralis Meek & Hayden. Meek, 1876, p. 196, Pl. 39, figs. 4a, 5a-c.

Description. Specimens 23.0 to 51.4 mm long, equivalve, inequilateral, umbones not prominent, more or less confluent with dorsal margin. Maximum inflation in dorsal third and along umbonal to posteroventral ridge, slightly anteriorly. Posterior end weakly truncated dorsally. Height, half width, anterior length and length of nymph, respectively, 60.1 to 71.6 (N = 14, μ = 66.2%), 10.9 to 20.8 (N = 14, μ = 15.2%), 45.7 to 50.4 (N = 14, μ = 47.9%) and 20 to 29 (N = 8, μ = 25%) percent of length. Shell thickest anterodorsally and dorsally, up to 2.0 mm thick over main disc, of two layers. A thin outer homogeneous or prismatic layer about one tenth the thickness of an inner complex cross-lamellar layer.

Other details given above.

Types. Lectotype of *Tellina equilateralis* Meek & Hayden, USNM 179, by subsequent designation of Meek (1876, in caption to Pl. 39, fig. 5b), a bivalved specimen, the right valve only exposed, shell incomplete and posterodorsal margin damaged, L=46.2, H=27.8, W=13.6, AL=21.2 mm. Type locality: mouth of Judith River, Montana. Stratigraphic position: Judith River Formation, Campanian.

Types held at YPM are: hypotypes YPM 24462-63, 24465-68; and 24464.

Discussion. As the measurements were made mostly on steinkerns, the height and half width to length percentages are probably lower than normal values. Values from steinkerns were not significantly lower than those based on specimens with shell. Both Meek (1876) and Landes (1940) considered equilateralis to be slightly inequivalve, the right valve being more convex. Inequivalveness is not evident in the Fox Hills samples. Landes considered that his specimens were distorted by compaction.

MATERIAL. 38 specimens, mostly articulated steinkerns (82.1%).

Occurrence. A rare species virtually restricted to Lower nicolleti Assemblage Zone (94.7%). The remaining two specimens were obtained from a float concretion that almost certainly came from the *Protocardia-Oxytoma* Assemblage Zone. Only three

concretions contained more than one specimen: A403 with six, A116 with three and A1357 with two.

Comparisons. Landes (1940, p. 157) recorded the presence of two cardinals on the poorly known left valve hinge of his specimens from the Bear Gulch "sandstone lentil" of the Pakowki Formation. He mistook the dorsal margin above the socket of 3b for a tooth. The characteristics of his shells, particularly the form of the umbones, right valve hinge, strong nymph, pallial sinus, internal dorsal ridge buttressing the anterior adductor, and the dimensions show that they are congeneric and probably conspecific with the Fox Hills specimens. Proof of their species relationship must await biometric studies.

"Tellina" parkerana Stephenson (1952) has only one triangular cardinal between two deep triangular sockets and one posterior lateral on the left valve. In general form and pallial sinus it is similar to equilateralis and may be congeneric. Should reexamination confirm this, then emendation of the generic diagnosis is required to include species with one or even no posterior lateral on the left valve, triangular cardinal teeth, and more prominent umbones giving a more trigonal shape. Species classed in Arcopagia, notably T. georgiana Gabb (Gardner, 1916, p. 692), are reported to have one cardinal tooth in the left valve. As the thin lamellar posterior lateral present on the left valve of many tellinids is easily broken off (Dall, 1900a) this should be checked carefully. If there is only one cardinal on the left valve hinge, georgiana may also be congeneric with equilateralis.

SOLENACEA

LEPTOSOLEN

AUTHOR. Conrad, 1865a, p. 184.

Type Species. By monotypy, Siliquaria biplicata Conrad (1858, p. 324, Pl. 34, fig. 17), from the Owl Creek Formation (Maestrichtian), Ripley, Tippah County, Mississippi.

Discussion. Conrad introduced *Leptosolen* as a subgenus of *Solena* Morchand but later (1867, p. 15) raised it to generic rank.

Leptosolen sp. indet.

One left valve steinkern (YPM 24746), incomplete ventrally and anteriorly and possessing some inner shell, has the typical shape and furrow, indicating the internal rounded rib, extending ventrally from the umbone, was collected from the *Crassostrea* bed at Loc. 75, A668, Hell Creek Formation.

HIATELLACEA

HIATELLA

AUTHOR. Daudin, in Bosc, 1801, p. 120.

Type Species. By monotypy (Dodge, 1950), Mya arctica Linnaeus (1767, p. 1113; = Hiatella biaperta Daudin + H. monoperta Daudin), Recent, Boreal and Indian Ocean.

Hiatella? sp. A (Plate 34, figs. 11–13)

DESCRIPTION. Small, specimens 9.5 to 24 mm long, equivalve, inequilateral. Umbones prominent, broad, prosogyrous. Subcylindrical, maximum inflation in dorsal third of shell. Maximum height at umbones. Shape variable, subrectangular, tapering slightly posteriorly, with a prominent umbonal to posteroventral angulation and a weak umbonal to posterodorsal ridge. Anterior end rounded. Posterior end subtruncate, the extremities rounded. Ventral margin convex, a slight posterior gape, no anterior gape. Height, half width and anterior length for N = 4, respectively, 53.3 to 62 ($\mu = 58.6\%$), 16.7 to 23.2 ($\mu = 20.1\%$) and 30 to 40 ($\mu = 35.9\%$) percent of length. Shell ornamented by irregular discontinuous weak costae crossed by oblique, short, raised striae.

Hinge narrow, apparently edentulous, with vague protuberances under the umbone in front of a small indefinite sunken ligament. Nymph opisthodetic, short and relatively strong. Adductor insertion areas weakly impressed, subequal, situated in dorsal third. Posterior adductor subquadrangular, separated by a narrow gap from a small elongated insertion area. Anterior adductor subrectangular, longer than posterior with a small dis-

crete oval insertion posteriorly above. Pallial line unknown.

Ostracum calcitic, cream-colored, relatively thick, about 0.2 mm thick on a specimen 14.8 mm long. Layering unknown.

Discussion. The shell form, inflation and prominent umbones favor classification in Hiatella. If the hinge is truly edentulous, as suggested by two rubber casts from poor specimens, the more correct placement may be under Cyrtodaria. Knowledge of the pallial line would aid placement.

MATERIAL AND OCCURRENCE. Rare, only four specimens. Three from the Little Eagle lithofacies, Lower nicolleti Assemblage Zone: YPM 24470, A529, Loc. 218; YPM 24471, A959, Loc. 104; YPM 24472, A1073, Loc. 243. One from the Hell Creek Formation: YPM 24688, A668, Loc. 75. The last, the largest specimen (24 mm long), has a more tapering posterior end.

PANOPEA

Author. Ménard de la Groye, 1807, p. 135.

Type Species. By subsequent designation of Children (1822, p. 84), Panopea aldrovandi Ménard de la Groye (1807, p. 136; a junior objective synonym of Mya glycimeris Born, 1778, p. 10), Recent, Mediterranean. See Vokes and Cox (1961).

Panopea occidentalis Meek & Hayden (Plate 35, figs. 1-3; Plate 28, fig. 14)

Panopaea occidentalis Meek & Hayden, 1856c, p. 270.

Glycimeris occidentalis (Meek & Hayden). Meek, 1876, p. 250, Pl. 39, figs. 9a,b.

[?]Panope webbi Warren, 1933, p. 117, Pl. 1, fig. 2.

[?]Panopaea simulatrix Whiteaves, 1885, p. 11, Pl. 2, figs. 2, 3.

[?] Panope borealis Warren, 1934, p. 91, Pl. 1, figs. 2, 3.

Description. Large, specimens 31.5 to 93.5 mm long, equivalve, inequilateral. Umbones anterior of center, prominent, prosogyrous. Shape compressed subquadrangular, greatest

height at umbones, maximum inflation dorsal, anterior to umbones, thinning posteriorly and anterodorsally. Height, half width and anterior length for N = 4, respectively, 57.1 to 62 (μ = 60.1%), 14.3 to 15.5 (μ = 14.7%) and 44.4 to 47.6 (μ = 46%) percent of length. Posterior end of valves strongly or moderately twisted out, giving a wide posterior gape. Anterior end gaping ventrally. Dorsal margin with a small gape anterior to umbones. Dorsal margins slightly concave, anterior end asymmetrically rounded, ventral margin sulcated posteriorly and posterior margin rounded with a weak sulcus ventrally. A broad sinus of variable prominence extends from below umbonal inflation to posterior part of ventral margin. Shell ornamented with concentric striae, lamellae and irregular growth ridges and depressions.

Hinge with one strong projecting cardinal tooth in each valve. Right valve cardinal anterior to tip of umbone, with a rounded front surface and a flat rear face. Left valve cardinal under tip of umbone, separated from nymph by a narrow deep socket, the anterior face flat, the rounded posterior surface with two or three plaits. Nymphs strong, large, 15.5 and 18.8 percent of length for two specimens. Musculation as for recent species. Adductor insertion areas equal, impressed, situated in dorsal half of shell, tear-drop-shaped, the posterior with a long narrow continuation under the hinge, the anterior with a similar shorter continuation (pedal retractors). A narrow pallial impression continues anteriorly halfway to umbone. Pallial line broad, with a shallow, narrow, asymmetric sinus.

Ostracum up to 3.5 mm thick. Layering unknown, although concentric cross-lamellar in part.

Types. Lectotype of *Panopea occidentalis* Meek and Hayden, USNM 180, by subsequent designation of Meek (1876, in caption to Pl. 39, fig. 9a), an incomplete bivalved gaping specimen, H = c.45 mm, $\frac{1}{2} \text{ W} = c.9 \text{ mm}$. Type locality: mouth of Judith River, Montana. Stratigraphic position: Judith River Formation, Campanian. Holotype of *Panope webbi* Warren, Univ. Alberta Ct. No. 554, by original designation, a left valve steinkern, L = 77, H = 46.5, $\frac{1}{2} \text{ W} = 10.5$, AL = 34.2 mm. Type locality: half a mile from mouth of Trapper Creek, Upper Peace River, British Columbia, Canada. Stratigraphic position: Smoky River Shale, "upper beds", Conacian.

Hypotype YPM 24469 held at YPM.

MATERIAL. Four specimens, one bivalved steinkern, one bivalved shell, and two right valve shells.

Occurrence. Rare, restricted to the *Tancredia-Ophiomorpha* Biofacies and the Irish Creek lithofacies where Waage found specimens in the life position.

Comparisons. Panopea species live deeply buried in the substrate and tend to be variable in shape and inflation. A reasonable number of specimens is required to define morphological variation. Two large specimens collected from the Tancredia-Ophiomorpha Biofacies are markedly different in the degree of outward flexure of the posterior end and the correlated size of the associated posterior sulcus (Pl. 35, fig. 1; Pl. 28, fig. 14). As most Upper Cretaceous species are based on one or a few specimens, generally poorly described and illustrated, determination of a synonymy is difficult. Panope webbi Warren is indistinguishable from the specimen of occidentalis. It lacks the strongly twisted-out posterior end, but the holotype (a steinkern) fits perfectly inside a shell from Loc. 49. The status of maclearni Warren (1934) is uncertain as it is reported to be edentulous. Well-preserved specimens of borealis may show it to be conspecific with occidentalis.

CYRTODARIA

Type Species. By subsequent designation of Vokes and Cox (1961, p. 186), Mya siliqua Spengler (1793, p. 48), Recent, Arctic seas.

Discussion. C. minuta sp. n., described below, differs from the type species by its more anteriorly situated umbones, more prominent anterior internal buttressing ridge, more distinct pallial sinus and a more definite sunken resilifer pit under the umbone. All these features are extremely variable on both siliqua and minuta. Such variation is typical of the burrowing, nesting or boring species of genera classed in the family. Thus minuta is placed tentatively in Cyrtodaria.

Cyrtodaria? minuta Speden, new species (Plate 35, figs. 4-11)

ETYMOLOGY. Referring to its small size.

Description. Small, specimens 6.5 to 12.0 mm long, equivalve, inequilateral. Umbones anterior, insignificant, weakly opisthogyrous or directed centrally. Shape variable, compressed subtrapezoidal, the greatest height posteriorly. Inflation variable, maximum posterior to umbones, sometimes close to posterior margin. Height at umbone, maximum height posteriorly, half width and anterior length for N = 12, respectively, 44.2 to 52.3 ($\mu = 48.2\%$), 48.9 to 58.3 ($\mu = 52.9\%$), 6.2 to 11.1 ($\mu = 8.2\%$) and 29.2 to 33.8 ($\mu = 31.7\%$) percent of length. Anterodorsal margin convex or angulated and weakly auriculate at extremity (Pl. 35, fig. 10), anterior end symmetrically rounded, ventral margin convex or weakly sinuous behind umbone, posterior margin rounded, subtruncate. Shell with a narrow lanceolate escutcheon, sometimes with a flattened dorsal area behind, a variable posterior gape and possibly an insignificant anterior gape. Ornamentation variable and irregular, of fine concentric striae, costae and undulations.

Hinge edentulous, slightly irregular below nymph. Nymph relatively large, extends about one third the length of dorsal margin posterior to beaks, its dorsal surface massive and filling escutcheon anteriorly, but thin and curving dorsally and more projecting posteriorly. A small sunken resilifer of variable prominence, sometimes elongated posteriorly, occurs below umbone at end of nymph. Adductor insertion areas subequal, moderately impressed. Anterior close to anterior margin, in dorsal half, narrow, bulbous with a thin dorsal prolongation. Posterior adductor in dorsal third, about one fifth to one sixth of length from posterior end, suboval with a small blunt dorsal protuberance (pedal retractor). A prominent small oval insertion area lies close to the umbone above the prominent internal rib extending from the umbone to the anterior adductor. Pallial line continuous, relatively wide, close to ventral margin, with a shallow asymmetric sinus or a weak indentation.

Ostracum thin, up to 0.15 thick, calcareous, layering indefinite, major part of shell with concentric cross-lamellar structure. Internal surface above pallial line with a few weak widely spaced narrow costae, strongest anteriorly, and rarely present on posterior adductor.

Types. Holotype YPM 24481, a bivalved specimen opened out so the valves are horizontal, as steinkerns and external impressions (Pl. 35, figs. 6–7), L = 8.6, H = 4.6, ½ W = 0.7, AL = 2.6 mm, Cymbophora-Tellinimera Assemblage Zone, Timber Lake Member. Paratypes: YPM 24483, right valve hinge (partly broken after photograph taken), shell and anterodorsal projection; YPM 24482, a left valve steinkern giving hinge; YPM 24485, a two-valved shell showing nymph and ornament; and 14 other paratypes, YPM 24484, 24486, 24667–78.

Discussion. The most variable parameter is inflation and the position of maximum inflation. Several valves show marked growth distortions in the form of depressions and grooves.

MATERIAL. 24 specimens, with and without shell.

Occurrence. Fourteen (58.4%) specimens come from the Lower nicolleti Assemblage Zone and five each from the *Protocardia-Oxytoma* and *Cymbophora-Tellinimera* assemblage zones. Only one concretion (A478; two specimens) contained more than one individual. Most specimens, although bivalved (12), are slightly displaced.

Comparisons. Corimya? sp., figured by Weller (1907, Pl. 37, figs. 14, 15), resembles minuta in shape and by its possession of anterior internal rib. Saxicava? albertensis Landes (1940, p. 163, Pl. 6, fig. 3), although poorly described and illustrated, has the same general shape and size. It has a thicker shell, concave basal margin, significantly greater inflation (23.1% for a right valve), and strong umbonal to posteroventral margin fold.

MYACEA

MYA

Author. Linnaeus, 1758, p. 670.

Type Species. By subsequent designation of Children (1822, p. 85), Mya truncata Linnaeus (1758, p. 670), Recent, Boreal seas.

Mya? sp. A (Plate 36, figs. 1–3)

Description. Specimens up to 40 mm long, equivalve, inequilateral. Umbones medial, low, compressed, apparently opisthogyrous. Subrectangular, height about 50 and half width about 20 percent of length, posterior end probably gaping. Maximum height at umbones, the posterior end narrower. Maximum inflation anterior, along a prominent rounded umbonal to anteroventral extremity ridge. The umbonal to posteroventral extremity ridge weak. Chondrophore of left valve strong, projecting, posteriorly directed, its surface details and inner margin unknown. Right valve hinge, musculation and pallial line unknown. Shell ornamented by weak concentric striae and undulations, constructed of concentric cross-lamellae which become complex cross-lamellar in umbonal region.

Types. Hypotypes YPM 24493-94.

Discussion. Because of the lack of good specimens and knowledge of internal morphology a new specific name is not given.

MATERIAL AND OCCURRENCE. Two incomplete articulated specimens, one incomplete right valve steinkern and one right valve external cast, all from the *Crassostrea* bed capping Dog Butte (Loc. 16), Colgate lithofacies, where it is very rare.

Comparison. The left valve from the Cannonball Formation identified by Stanton (1920, p. 32) as "Panope simulatrix Whiteaves?" resembles the poor specimens from Dog Butte. Cvancara (1966, p. 341, Pl. 8, fig. 15) refigured and discussed the specimens from the Cannonball Formation.

VARICORBULA

AUTHOR. Grant and Gale, 1931, p. 420, footnote 1.

Type Species. By original designation, Tellina gibba (Olivi, 1792, p. 101), Recent, west coast of Europe and the Mediterranean Sea.

Discussion. This is the Corbula of many authors. The authorship of Corbula and the selection of a type species have been extensively debated (Gardner, 1926, 1928; Vokes, 1945b; Burch, 1960). Under articles 11 (c) (ii) and 16 (a) of the International Code of Zoological Nomenclature (Stoll and others, 1964) Bruguière's (1797) Plate 230 is an acceptable valid indication (cf. Vokes, 1945b). Corbula nucleus Lamarck (1818, p. 496, = C. gibba (Olivi)) was not proposed until 1818 and, as mentioned by Vokes (p. 8), is not available as a type species, especially as there is no reason why Schmidt's (1818, p. 77, 177) designation of C. sulcata Lamarck (1801) should not be considered valid. It could be argued that the only species on Bruguière's plate then named should be selected as the type species. Vokes' (1945b) usage of Corbula and Varicorbula is followed here.

Varicorbula crassimarginata, decribed below, has the shape and hinge characters of the genus, but it resembles Caryocorbula by the buttressing of the posterior adductor scar and the tendency to have a posterior angulation and concentric costae on both valves.

Varicorbula crassimarginata (Meek) (Plate 36, figs. 4–13, 15)

Corbula crassimarginata Meek & Hayden, 1860b, p. 425 (nomen nudum). Meek, 1876, p. 244, Pl. 17, figs. 14a-c.

Description. Small, specimens 4.1 to 7.1 mm long, inequilateral, inequivalve, the left valve smaller and fits into a groove around the margin of the right valve. Dorsal margins of right valve overlap those of the left valve. Moderately inflated, maximum inflation about mid-height, sometimes lower when the ventral margin curves in sharply. Maximum height at umbones. Umbones prominent, low, prosogyrous. Right valve umbone projects only slightly above that of the left valve. Ventral extension of the right valve, which is small when the margins reflexes sharply inward, makes up most of the inequivalveness. Shape subquadrangular to subtrapezoidal, anterior end rounded, sometimes tapering, posterior end subtruncated, posteroventral extremity subangular to pointed. Height, half-width and anterior length of left valve, respectively, 66.7 to 79.5 (N = 15, μ = 72.9%), 19.3 to 29.6 (N = 14, μ = 25.6%) and 36.6 to 44.7 (N = 14, μ = 40.7%) percent of length. The same parameters for the right valve for N = 9, respectively, 68.6 to 79.6 $(\mu = 72.7\%)$, 21.3 to 27.8 ($\mu = 24.4\%$) and 36.1 to 42.6 ($\mu = 38.9\%$) percent of length. Length, height and width of right valve, respectively, 103.8 to 107 (N = 4, μ = 105.7%), 110.3 to 112.5 (N = 4, μ = 111.3%) and 100 to 122.2 (N = 9, μ = 108.7%) percent of the matching left valve measurements. Both valves with a prominent umbonal to posteroventral ridge. Posterodorsal margin of left valve with a sharp incurving costa outside area of overlap of the right valve, sometimes with a weak sulcus between this and the umbonal ridge. Ornamentation variable, of fine concentric striae and/or irregular weak costae, or strong sharp-crested costae, separated by wider interspaces, on the ventral half or most of the right valve and less frequently on the ventral part of the left valve.

Cardinal tooth of right valve strong, conical, curves dorsally, sited in front of a relatively wide internal resilifer that extends up under umbone. Chondrophore of left valve strong, projecting, the posterior two thirds of its surface occupied by a raised concave resilifer. A prominent nodular boss posterior to the resilifer fits into a socket

posteroventral to the resilifer of the right valve. Socket for cardinal tooth of right valve deep, extends under and is separated from umbone by the thin anterior end of chondrophore. Adductor insertion scars moderately impressed, subequal. Anterior close to anterodorsal margin, elongate-elliptical, narrows dorsally and curves posteriorly, with a more strongly impressed small oval pedal retractor fused to its dorsal margin. Posterior insertion larger, subquadrangular, on a raised buttress, its dorsal margin impressed and perhaps representing the posterior pedal retractor. Pallial line relatively wide and remote from margins, joins internal ventral extremities of adductors, broken into segments by narrow gaps. Ventral part of posterior vertical limb with a shallow asymmetric pallial sinus.

Ostracum relatively strong, of variable thickness, up to 0.4 mm thick, of two layers of approximately equal thickness over main disc of shell. An outer concentric cross-lamellar layer and an inner complex cross-lamellar layer. Ventral margin of right valve below socket for left valve sometimes overthickened. The surface above the pallial line may have weak, narrow, widely spaced radial striae.

Types. Lectotype of Corbula crassimarginata Meek, USNM 299, by subsequent designation of Meek (1876, in caption to Pl. 17, fig. 14b), a closed steinkern with some inner shell, L=4.9, H=3.8, W=3.2, AL=2.0 mm. Type locality: Moreau River, South Dakota. Stratigraphic position: Fox Hills Formation.

Hypotypes YPM 24495–98 are held at YPM.

Discussion. A large sample of the Recent V. gibba (YPM 813) shows the same range of shape and ornament variation. The strength of its umbonal to posteroventral ridge is also variable, but no specimens have a sharp keel comparable to one specimen (YPM 24496; Pl. 36, figs. 5, 8) placed in crassimarginata. Because it is similar to other specimens in shape other than the pointed posteroventral extremity, which correlates with the keel, posterodorsal ridge and ornament, and as a normal specimen occurred close to it in the same concretion the specimen is considered to be an aberrant form.

The easy loss of the outer shell layer, with the accompanying loss of the ventral band of the right valve, almost certainly accounts for Meek's (1876, p. 245) considering the species to be approximately equivalve.

MATERIAL. 32 specimens.

Occurrence. Rare, two specimens from the *Protocardia-Oxytoma* Assemblage Zone at Loc. 121, one from the Trail City Member above *Protocardia-Oxytoma* Assemblage Zone and all but one (Loc. 184) of the remainder from the vicinity of the Moreau River west of Route 63 in both the *Cucullaea* (65.6%) and *Cymbophora-Tellinimera* assemblage zones. Only rarely were two individuals found in one concretion. Three were collected from one.

There is no record of crassimarginata outside the type area of the Fox Hills Formation.

Comparisons. Meek and Hayden's (1860b, p. 425) listing of the name Corbula crassimarginata does not constitute a valid indication. The species is to be attributed to Meek (1876). No closely related species appears to have been described from the Upper Cretaceous of the Western Interior. Most of the descriptions and illustrations are inadequate and revision, preferably based on additional specimens, is required. Corbula lactana Landes warrants close comparison to crassimarginata.

CORBULAMELLA

Author. Meek & Hayden, 1857, p. 142.

Type Species. By original designation, Corbula? gregaria Meek & Hayden (1856a, p. 84). Upper Cretaceous (Campanian-Maestrichtian), Western Interior, U.S.A.

Discussion. Vokes (1945b), in his revision of the supraspecific taxa of the Corbulidae, redescribed the type species and instituted a new subfamily, the Corbulamellinae. The extremely variable and aptly named type species is described in considerably more detail below.

Corbulamella gregaria (Meek & Hayden) (Plate 36, figs. 14, 16–21; Plate 37, figs. 1–6)

Corbula? gregaria Meek & Hayden, 1856a, p. 84.
Corbulamella gregaria (Meek & Hayden). Meek & Hayden, 1857, p. 143. Meek, 1876, p. 247, Pl. 17, figs. 13a-d. Vokes, 1945b, p. 19, Pl. 2, figs. 21–26.
Corbula inornata Meek & Hayden, 1858, p. 52. Meek, 1876, p. 245, Pl. 30, figs. 4a-d.

Description. Small, specimens 1.6 to 3.6 mm long, inequilateral, strongly inequivalve, the left valve smaller, and all of its margin, except near the umbone and resilifer, fits into a continuous groove on the right valve. Anterior and posterior dorsal margins of left valve thin, upturned to fit in sockets in the strongly overlapping margins, especially the posterior, of the right valve. Maximum height at umbone. Maximum inflation in dorsal half. Umbones prominent, tumid, incurved, prosogyrous, the right valve umbone projecting above and almost touching that of the left valve. Shape extremely variable, subquadrangular to subtrigonal, the left valve characteristically subquadrangular and the right valve subtrigonal.

Height, half width and anterior length of left valve, respectively, 82.1 to 100 (N = 70, $\mu = 91.1\%$), 29.4 to 42.9 (N = 69, $\mu = 35.6\%$) and 40.9 to 50 (N = 69, $\mu = 46.5\%$) percent of length. Same parameters for the right valve, respectively, 88.5 to 100 (N = 19, $\mu = 96.3\%$), 33.3 to 48.1 (N = 19, $\mu = 40.8$) and 40 to 48.3 (N = 19, $\mu = 44.8\%$) percent of length. Length, height and half width of right valve, respectively, 106.7 to 112.5 (N = 15, $\mu = 109.4\%$), 107 to 124 (N = 14, $\mu = 115.8\%$) and 100 to 130 (N 67, $\mu = 114.9\%$) percent of left valve measurements. Height of right valve above base of left valve is 104 to 118.1 (N = 50, μ = 110.2%) percent of height of left valve. A vague heart-shaped anterodorsal area is defined by weak umbonal to anterodorsal extremity ridges. Posterior dorsal margin of right valve thickened and swollen, with strong ornament, sometimes bordered below by a weak or strong sulcus which may sulcate the normally convex posterodorsal margin. Posterodorsal margin of left valve with a weak or strong and frequently rugose ridge outside line of overlap of the right valve, bordered below by a strong to weak sulcus that normally sinuates the posterior margin and gives the left valve its subquadrate shape. Ornament extremely variable. Generally with weak concentric striae and ridges on the left valve and umbonal half of right valve, but sometimes with strong flat-topped costae separated by narrow interspaces on the ventral half of the right valve. Both valves sometimes virtually smooth with only faint striae, or with strong costae, or the right valve may be costate for most of its height.

Right valve with one strong conical cardinal tooth below umbone and in front of an internal triangular prosoclinal resilifer pit that dorsally has a small overdeepened part for the outer ligament layer. Directly behind the resilifer the ventral margin of the hinge has a weak socket for the end of the chondrophore of the left valve. Left valve with a deep conical socket anterior to umbone above which the dorsal margin is thickened and fits into an enlargement of the marginal socket above the cardinal tooth of the right valve.

Resilifer shallower and smaller, borne on a strong thin chondrophore plate extending prosoclinally upward from posteroventral margin of conical socket. On an internal view of interlocking valves the chondrophore appears as a larger quadrangular cardinal tooth. Relatively strong semi-elliptical "lamellae" project into the mantle cavity from below posterior part of hinge in dorsal third of the shell.

Adductor insertion areas subequal, weakly impressed, especially the posterior. Anterior close to anterodorsal margin, lower than posterior, sausage-shaped with a more deeply impressed small oval insertion (pedal retractor) fused to dorsal margin. Posterior adductor slightly larger, subelliptical, occupies most of dorsal surface of lamella. Under the hinge above the anterior end of the posterior adductor is a small deeply impressed pedal retractor insertion. Pallial line relatively wide, remote from posterior and ventral margin, posterior limb almost vertical and has a small shallow asymmetric sinus in ventral half.

Ostracum variable in thickness on different specimens, less than 0.1 mm thick, of two layers of approximately equal thickness over main disc of shell. An outer concentric cross-lamellar layer and an inner of concentric or complex cross-lamellar structure. Margins of the right valve external to the socket for the left valve are very thin and fragile. Ventral margin of right valve with a weak ridge below socket for margin of left valve. Sometimes present is a weak ridge extending from base of umbone to near dorsal end of anterior adductor.

Types. Lectotype of *Corbula? gregaria*, by subsequent designation of Meek (1876, in caption to Pl. 17, fig. 13a), a bivalved specimen; not located in collection USNM 355. Type locality: Yellowstone River, 150 miles above mouth, Montana. Judith River Formation, Campanian. Lectotype of *Corbula inornata*, by subsequent designation of Meek (1876, in caption to Pl. 30, fig. 4a), whereabouts unknown. Type locality: Long Lake near Fort Pierre, North Dakota. Stratigraphic position: Fox Hills Formation.

Hypotypes YPM 24157-58, 24160-64, 24166-68; and other types YPM 24159 and

24165 are held at YPM.

Discussion. The marked variability of gregaria is perhaps largely due to its gregarious, probably byssally attached mode of life. Because of the inequivalveness and the fragility of the margins, perfect specimens of the right valve are difficult to obtain. Breakage of the margins peels off most of the outer shell layer, making specimens appear smooth when they may have had strong concentric ornament. The left valve is normally well preserved and is made the standard of reference for the measurements. Size-frequency histograms approach a bell-shaped curve, probably because of the species' small size and short life (approximately two years for many corbulid species; Baĉesco and others, 1957) (Fig. 18).

MATERIAL. About 10,000 specimens, including 3128 selected systematic specimens, as individuals and in sample blocks.

Occurrence. Virtually restricted to the *Limopsis-Pseudoptera* Assemblage Zone (99.6%) where it occurs as thousands of individuals dominating a concretion or, more commonly, as a codominant with *Limopsis* and *Pseudoptera* when it may be scattered throughout or restricted to a patch in a concretion. Single valves and steinkerns are uncommon. Only 112 (1.1%) of the counted specimens are single valves. Right valves are more numerous but not significantly so in all samples counted. Many specimens are bored, the extreme being in A305 where 34.6 percent of 332 individuals were bored. Some had holes in both valves or occasionally two holes in one valve.

Corbulamella gregaria has been recorded from four localities, the Yellowstone River, type area of the Fox Hills, Belle Fourche River (Vokes, 1945b), South Dakota and "Long Lake" (as inornata; Meck, 1858, p. 52), North Dakota.

Comparison. This distinctive species is unlikely to be confused with any other Upper Cretaceous bivalve. Specimens of *Corbula inornata* figured by Meek (1876) closely resemble *gregaria*. Meek stressed the ventral concordance of the valves and the smooth surface but these are probably due to the lack of the outer shell layer. He (in Meek and Hayden, 1858, p. 52) noted the presence on steinkerns of a distinct groove in the position of the "lamella" of *Corbulamella* and suspected that *inornata* might belong in the genus.

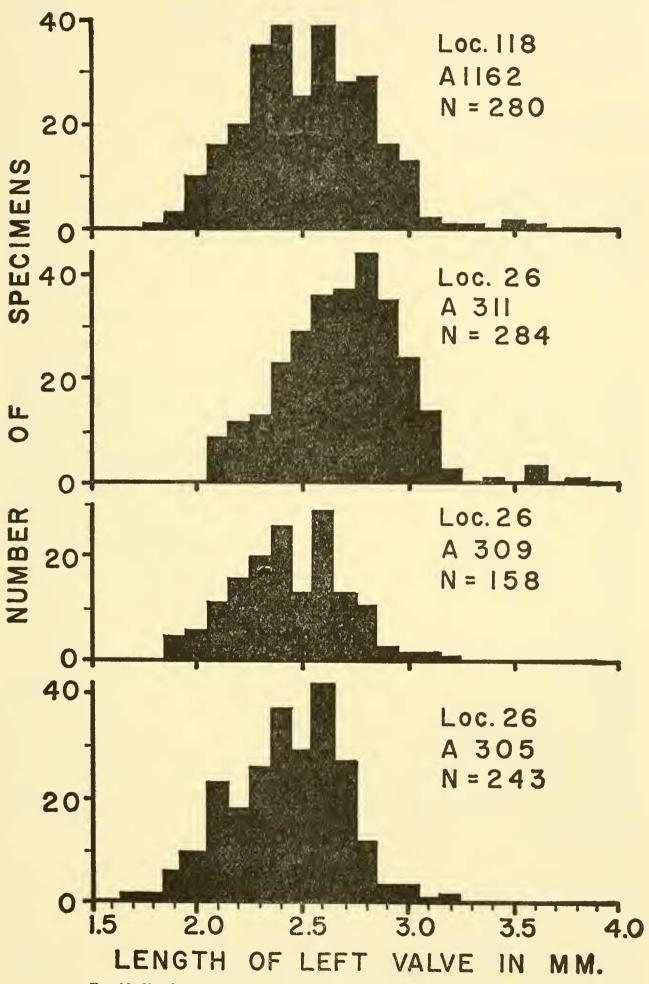


Fig. 18. Size-frequency histograms of samples of Corbulamella gregaria.

C. inornata here is considered conspecific with gregaria. Recollections from the type locality or the original collection are required to prove equivalence.

PHOLADACEA

PARAPHOLAS

AUTHOR. Conrad, 1848, p. 121.

Type Species. By monotypy, *Pholas californica* Conrad (1837, p. 236, Pl. 18, figs. 5–6), Recent, southern California coast.

Parapholas sp. A (Plate 37, figs. 7, 8)

Description. Large, 48.7 mm long, 30.8 mm high, half width 14.8 mm and anterior length 6.8 mm. Equivalve, inequilateral. Anterior end very inflated, maximum inflation in dorsal half below umbones, tapering posteriorly. Maximum height at umbones. Umbones tumid, incurving, weakly opisthogyrous. Shape typical of genus. Posterior end asymmetric, more gradually rounded above, closed. Anterior slope with 11 sharp-crested radial plicae, strongest anteriorly and faint posteriorly, knotted where crossed by concentric plicae, the interspaces round-floored and about twice as wide as plicae. Disc and posterior slope with concentric striae, costae and plicae, the plicae strongest on the disc, the others more crowded and stronger on the posterior slope. Callum relatively small, ornamented by plicae, and possibly striae and costae. Umbonal-ventral ridge and sulcus strong, sharp and projecting, bordered posteriorly on external surface by a furrow. Umbonal to posteroventral extremity ridge rounded, weak. Accessory plates absent, but the anterodorsal margins have projections that probably represent part of an umbonal reflection.

Hinge and internal features unknown. Shell up to 0.7 mm thick, apparently consisting mainly of concentric cross-lamellar structure.

Discussion. The morphological terms followed are those of Turner (1954, 1955), who noted (p. 3, 123) that the genus is not found living in the western Atlantic. This specimen and the two recorded as Martesia tumidifrons by Whiteaves (1889, p. 179) are the oldest known members of the genus in North America, and possibly the world. Fused or close adherence of the inner shelf of the dorsal extension is suggested by smooth rounded surface between the anterodorsal margins of the valves on the steinkern (Pl. 37, fig. 8). A series of small discrete protuberances near the ventral margin of the steinkern anterior and posterior to the umbonal-ventral ridge marks the position of a ventral adductor scar. Parapholas acuminata (Sowerby) has a similar ridged scar that extends farther posteriorly.

MATERIAL AND OCCURRENCE. One specimen (YPM 24492) from Loc. 73 (A653), Cucullaea Assemblage Zone, Irish Creek lithofacies. Most of the shell is missing anteriorly, ventrally and posteriorly on the left valve.

COMPARISON. Parapholas tumidifrons (Whiteaves, 1889, p. 179, Pl. 25, figs. 1, 1a, 2) has the general shape and dimensions but much weaker, fewer and less curved anterior radial costae which are not impressed on steinkerns. The differences may not be of specific rank.

OPERTOCHASMA emend.

Author. Stephenson, 1952, p. 139.

Type Species. By original designation, Opertochasma venustum Stephenson (1952, p. 139, Pl. 34, figs. 13–16), from the Woodbine Formation (Cenomanian), Texas.

EMENDED DIAGNOSIS. Small- to medium-sized, subconical, maximum inflation below and maximum height at umbones. Umbones prominent, strongly incurved, the tips pointing outward, prosogyrous. Anterior gape confined to ventral half of height, subtrigonal, its dorsal margins concave giving dorsally directed apices at dorsal extremities and commisure, covered in adult forms by non-fused callum plates which are raised above the level of the anterior slope and leave a small or negligible gape. Mesoplax (= protoplax of Stephenson) of two plates, combined general form as for Martesia, strong, suboval to subquadrangular, the anterior lateral margins concave to fit onto top of umbonal reflection projections (Pl. 37, fig. 13), smooth on dorsal surface, costate on ventral surface. Dorsal gape wide, filled by partly calcified periostracum, the gap between the valves covered by a thin, narrow, lanceolate metaplax which arches upward dorsally to fit a convexity behind umbones. A similar but shorter hypoplax covers the ventral junction of partially calcified periostracum. Posterior end of shell chitinous, externally with strong to weak irregular plicae, internally initially with strong growth flanges (as in Martesia striata Linnaeus), passing posteriorly into a long siphonal tube consisting of an outer periostracum and over much of its length an inner prismatic calcareous layer. Conical pit under umbonal reflections prominent. External umbonal-ventral sulcus narrow, steep-sided, shallow to deep, matched internally by a strong raised rib, both knotted or raised where crossed by plicae or costae. A weak condyle is present at base of the internal rib. A second shallow or deep sulcus, anterior to the former, passes either directly from umbones to ventral margin or curves forward to the margin of the callum which it follows ventrally, producing a step-down to the anterior above the callum and a stepup to the callum. This anterior sulcus is matched internally by a low rib. A weak to strong, broad, flat-topped rib of variable length, extending halfway almost to the ventral margin, occurs on the inside of the shell under the posterior umbonal ridge. A narrow short costa is sometimes present between the broad rib and the posterior adductor scar. Callum smooth. Anterior slope with fine plicae or costae which follow the inner margins of the callum, their crests thin, pointing dorsally, smooth or crenulated. Disc with weaker ornament, sometimes of coarser plicae. Posterior slope smooth or with imbricating scales.

Apophyses rodlike, as in *Martesia*. Muscle insertion areas impressed. Posterior adductor insertion elongate-rectangular, narrow, near posterior part of dorsal margin. Ventral adductor muscle insertion irregular, mostly elongate-elliptical, mainly posterior to umbonal-ventral rib but sometimes extends slightly anterior to it. Accessory anterior adductor muscle insertion area irregular pear-shaped, more swollen dorsally, above callum close to anterodorsal margin. Above and posterior to it is a larger, subcircular anterior adductor scar which overlaps onto the inner surface of umbonal reflection. Posterior to umbonal ventral rib the pallial line is continuous. Pallial sinus shallow, asymmetric. Pallial line anterior to the rib consists of discrete irregular oval to elliptical scars that follow margin of callum.

Discussion. Stephenson (1952) correctly included "Martesia" cuneata (Meek & Hayden) in his new genus. Abundant well-preserved specimens of O. cuneatum permit emendation of Stephenson's diagnosis, especially the addition of musculation information and the occurrence of a hypoplax. In addition to those features listed by Stephenson, Opertochasma differs from Martesia by its discontinuous anterior pallial line and longer and narrower ventral and posterior adductor scars. The gross morphological resemblance

of Opertochasma to Martesia places it in the Martesiinae (Turner, 1955) and suggests that it may have been ancestral to Martesia. Meek (1876, p. 256) did not observe any callum plates on numerous specimens of Turnus (Goniochasma) stimpsoni (Meek & Hayden) and, if adult, it cannot belong in the Martesiinae.

Opertochasma cuneatum and Stephenson's species are discussed below.

Opertochasma cuneatum (Meek & Hayden) (Plate 37, figs. 9–16; Plate 38, figs. 1–5)

Pholas cuneata Meek & Hayden, 1858, p. 53.

Pholas (Martesia) cuneata Meek & Hayden. Meek & Hayden, 1860b, p. 424.

Martesia cuneata (Meek & Hayden). Meek, 1876, Pl. 30, figs. 8a,b.

Opertochasma cuneatum (Meek & Hayden). Stephenson, 1952, p. 139.

DESCRIPTION. Small, specimens 2 to 16 mm long, equivalve, inequilateral. Subconical, posterior end tapering, bluntly rounded, umbones and general form as described above. Height, half width and anterior length for N = 47, respectively, 30.5 to 60 (μ = 45%), 15.4 to 28.6 ($\mu = 20.4\%$) and 9 to 20.6 ($\mu = 14.8\%$) percent of length. Anterior sulcus externally weak or absent, marked internally by a weak to strong rib. Anterior slope in front of sulcus ornamented by narrow closely spaced sharp-crested costae, the crests projecting dorsally and sometimes lamellar, strongest and more widely spaced near sulcus. Anterior slope between sulci with low plicae which are strongest and widest posteriorly. Disc with semiregular low plicae, weakening and sometimes absent posteriorly. Posterior. slope and periostracal parts smooth or with a few weak irregular plicae. Siphonal tube long. Umbonal-ventral sulcus narrow, deep, its matching internal rib very projecting, both knotted where crossed by plicae. Anterior sulcus shallow, curves from umbone to inner projection of callum which it follows to ventral margin, sometimes very weak. Internal posterior flat-topped ridge adjacent to posterior umbonal margin normally strong, sometimes indefinite. Mesoplax subcircular to suboval, about as wide as long, the anterior lateral margins concave to fit into umbonal reflections. Metaplax, hyoplax, internal ribs, adductor muscle insertions and pallial line as described in diagnosis.

Ostracum thin, up to 0.4 mm thick, mostly 0.2 to 0.3 mm, consisting of a thick inner concentric cross-lamellar layer, a prismatic layer and an outer chitinous layer, locally calcified, especially on inner surface near posterior dorsal and ventral margins and on the siphonal tube.

Types. Lectotype of *Pholas cuneata* USNM 455, by subsequent designation of Meek (1876, caption to Pl. 30, fig. 8a), a bivalve closed steinkern, the anterior end of the left valve crushed, L = 9.8, H = 4.6, W = 4.1 mm. Type locality: Long Lake, North Dakota. Stratigraphic position: Fox Hills Formation.

Hypotypes YPM 24478-80, 24488-91 and 24499 are held at YPM.

Discussion. The measurements are based on a sample from one tree stem (A943, Loc. 95). Unweathered specimens are well preserved. Many retain periostracum. With death the chitinous parts tended to collapse, so distorting individuals. There is considerable shape variation which is to be expected of a normally densely crowded wood-boring species (Turner, 1954, p. 14).

MATERIAL. About 1500 individuals, all articulated, mostly in place in wood.

OCCURRENCE. Restricted to boring in small or large wood fragments, either radially or horizontally aligned to growth axis of the stem (P1. 38, fig. 1). Most stems are inhabited by one size group (spatfall). A few large stems contain a size range possibly indicating more than one spatfall. Yet the presence of callum plates on the smallest specimens

(L = 2 to 5 mm) suggests that the size range might be due to accelerated growth under conditions of crowding (Turner, 1954, p. 6). The stratigraphic range of the species is from the Lower *nicolleti* Assemblage Zone, Trail City Member to the Cymbophora-Tellinimera Assemblage Zone, Timber Lake Member. It is common only in the Lower *nicolleti* Assemblage Zone (56.8%).

Comparisons. Stephenson (1952) included two new species, O. venustum (USNM 105594) and subconicum (USNM 105597), in his new genus. The anterior radial sulcus is sometimes weak (as on cuneatum) or lacking (on subconicum) and, as the shape and ornament differences used by Stephenson to distinguish the species are minor and probably phenotypic, the two species are here considered conspecific. Opertochasma cuneatum, compared to venustum, is longer and more slender, its anterior sulcus is more remote from the umbonal-ventral sulcus and curves toward the callum and does not pass straight down to the ventral margin, its ornament on the anterior slope is stronger and more widely spaced, the disc has strong concentric plicae, especially near the sulcus, and the posterior slope is smooth not scaly.

The generic status of many other Upper Cretaceous pholadids requires revision.

Martesia cretacea (Gabb) has the same shape and two sulci, close together, passing

ventrally from umbone. It is probably an Opertochasma.

PANDORACEA

PERIPLOMA

AUTHOR. Schumacher, 1817, p. 115.

Type Species: By monotypy, Periploma inaequivalvis Schumacher (1817, p. 116), Recent, West Indies.

Periploma subgracile (Whitfield) (Plate 38, figs. 6-8)

Thracia subgracilis Whitfield, 1877, p. 36. Whitfield, 1880, p. 419, Pl. 11, figs. 29, 30. [?] Anatina subgracilis (Whitfield). Stanton, 1920, p. 26, Pl. 3, figs. 4a,b, 5a,b. [?] Laternula? subgracilis (Whitfield). Cvancara, 1966, p. 357, Pl. 9, figs. 19, 20. [?] Periploma johnseni Landes, 1940, p. 150, Pl. 4, figs. 4, 5. [?] Periploma sp. Cvancara, 1966, p. 355, Pl. 9, figs. 17, 18, 23, 26.

Description. Specimens 8.3 to 34.5 mm long, equivalve or subequivalve, inequilateral, compressed. Umbones posterior, moderately prominent, incurved, opisthogyrous. Maximum inflation anterior to umbones, in dorsal half, thins rapidly posteriorly. Shape subtrapezoidal, anterior end and ventral margin broadly rounded. Posterior end tapering, narrowly or broadly rounded, sometimes slightly truncated posterodorsally, weakly twisted toward the right valve and possibly slightly gaping. Posterior dorsal margin straight or concave. Height, half width and anterior length, respectively, 68.5 to 78 (N = 7, μ = 71.9%), 13 to 15.7 (N = 7, μ = 14.6%) and 58.8 to 68.2 (N = 7, μ = 64.4%) percent of length. Shell ornamented by faint irregular concentric striae and raised lines, and sometimes with narrow or broad weak irregular plicae.

Hinge poorly known, apparently characteristic of genus. Each valve with an internal spoon-shaped resilium, buttressed posteriorly by a strong rib. Beaks fissured internally with an adjacent weak ridge on posterior side. Musculation as for genus. Adductor insertion areas unequal. Posterior close to umbones, above buttress, small, impressed,

subquadrangular, the anterior margin concave or straight, with a short blunt projection (pedal retractor) extending from the anterodorsal extremity. Anterior adductor in dorsal half of shell, close to margin, long, and narrow. A small oval insertion area is present close to dorsal margin halfway between anterior adductor and umbone. Pallial sinus broad, not quite extending to umbones, forming a sharp posterodorsally curving projection where it meets the pallial line. Remainder of pallial line close to ventral margin.

Ostracum thin, up to 0.2 mm thick, of two layers. A thin outer gray translucent homogenous or prismatic layer, its outer surface subvitreous, and an inner subnacreous layer two to three times thicker. The latter layer has internal weak radial striae which are

sometimes evident on inner surface of shell.

Types. Lectotype of Thracia subgracilis, USNM 12253, by subsequent designation of Stanton (1920, p. 27, Pl. 3, fig. 4a), a bivalve steinkern with some inner shell, L = 19.8, H = 14.4, W = 7.1, AL = 11.6 mm. Type locality: Cheyenne River, near French Creek, Black Hills, South Dakota. Stratigraphic position: "Probably from near top of No. 4" (Whitfield), Pierre Shale, Upper Cretaceous, Campanian. Holotype of Periploma johnseni Landes, Geol. Survey Canada Cat. No. 9353, by original designation. Type locality: Milk River, Alberta, in SE 1/4 sec. 21, T.2, R.7, W.4th Meridian. Stratigraphic position: Foremost Formation, Campanian-Maestrichtian.

Hypotypes YPM 24154-56 are held at YPM.

Discussion. Small specimens generally lack concentric plicae. Measurements from two bivalved specimens indicate that the species is essentially equivalve. The left valve of other disarticulated specimens appears to be very slightly more compressed. The inflation of the type specimen and of one from the Cannonball Formation, quoted by Stanton (1920), are respectively 17.5 and 18.8 percent of length and exceed the maximum value recorded above.

MATERIAL. 17 specimens, mostly steinkerns. Some retain shell.

Occurrence. All but one specimen of this rare species were collected from the Timber Lake Member. Twelve came from the *Cymbophora-Tellinimera* Assemblage Zone. No more than two specimens came from any concretion. Only one single valve was collected. Most of the bivalved specimens were disarticulated but still associated, to varying degrees.

Comparisons. Landes distinguished his *P. johnseni* from *subgracile* by its more oval outline, especially the broad rounded posterior end, lack of concentric undulations, the more posterior beaks, and possibly its larger size. Yet he mentions that some specimens have "a rapidly ascending posterior basal margin" and so resemble *subgracile*. The absence of shell emphasizes the posterior narrowing. Landes' differences are probably phenotypic and another species name is unwarranted. The specimens of *Periploma* sp. and *Laternula? subgracilis* (Whitfield) illustrated and described by Cvancara (1966) apparently do not differ from the Fox Hills specimens.

Comparison of the species discussed is hampered by the paucity of specimens and

their poor preservation.

PHOLADOMYACEA

PHOLADOMYA

AUTHOR. G. B. Sowerby, 1823, pt. 19, on 225th and 226th unnumbered pages, Pl. 37.

Type Species. By subsequent designation of Gray (1847, p. 194), Pholadomya candida Sowerby (1823, Pl. 37), Recent, West Indies.

Pholadomya deweyensis Speden, new species (Plate 38, figs. 9-11)

ETYMOLOGY. From Dewey County, South Dakota.

Description. Medium size, specimens 4.3 to 29.2 mm long, equivalve, inequilateral. Umbones tumid, prominent, prosogyrous, at about anterior quarter. Maximum height at end posterior to umbones. Maximum inflation in dorsal third, decreases steadily ventrally and toward extremities. Dorsal surfaces distinct, the posterior feebly concave. Shape suboval, moderately inflated, consistent. Height, half width and anterior length for N = 6, respectively, 71.3 to 76.1 ($\mu = 73.5\%$), 22.5 to 25.9 ($\mu = 24\%$) and 23.1 to 28.8 ($\mu = 26.3\%$) percent of length. Posterodorsal margin straight or weakly convex. Dorsal part of posterior end straighter than ventral part. Anterior end broadly rounded, forms an almost continuous curve with the ventral margin and the ventral part of the posterior margin. Posterior gape small, most open dorsally. Shell ornamented with 16 to 20 round-topped, prominent radial plicae separated by shallow flat-floored interspaces about 1.5 times as wide. One or two secondary plicae may intercalate on center part of disc. Plicae become more widely spaced at extremities, weaken in dorsal third of height, absent from the narrow anterior and posterior dorsal areas. Radial plicae crossed by concentric plicae, 25 and 27 respectively on specimens 23.8 and 29.2 mm high, and by fine concentric raised striae that are thickest over the radial plicae. Radial plicae widest and nodular, especially at extremities and ventrally, where crossed by concentric plicae. Concentric plicae irregular and indefinite on first 2 to 3 mm height.

Hinge narrow, with a low, elongated narrow protuberance extending prosoclinally under end of nymph from end of anterior margin, and defining the ventral limit of a shallow resilifer sunken under and behind the umbone. Nymph, the thickened margin of the valve, very short, relatively strong, carries an external opisthodetic ligament. Muscle insertion areas and pallial line unknown. Ostracum very thin, less than 0.1 mm thick except along hinge, of two layers. A thin outer clear apparently homogeneous or prismatic layer, and an inner lamellar layer with a silvery luster.

Types. Holotype, YPM 24152, a right valve steinkern, L = 29.2, H = 21.7, 1/2 W= 6.8, AL = 7.1 mm, from the *Protocardia-Oxytoma* Assemblage Zone, Trail City Member. The associated left valve was partly destroyed to expose the right valve. Paratypes: YPM 24151, a crushed and incomplete disarticulated bivalved specimen giving the central part of the hinge; YPM 24153, a left valve with umbonal shell preserving part of the nymph; and 16 other paratypes, YPM 24679-87, 24689-95.

Discussion. The number of radial plicae is very consistent for specimens from different assemblage zones and members. The variation is due partly to the intercalation of secondary plicae which rapidly become as prominent as the primaries. Most specimens break away, leaving the outer shell layer attached to the external mould and the inner shell layer to the steinkern.

MATERIAL. 34 specimens, mostly steinkerns.

Occurrence. A rare species relatively common in the Lower *nicolleti* Assemblage Zone (53.3%). For stratigraphic distribution see Figure 4. Mainly one specimen, rarely two, per concretion. Single valves are the more numerous, and because of the fragility of the shell many are crushed by compaction or broken during transportation. One quarter of the specimens are bivalved.

Comparisons. Morphological variation of Pholadomya species has long plagued paleontologists, resulting in excessive splitting or lumping (see Arkell, 1935, p. 330). Considerable variation could be expected in species of a genus following a burrowing or boring mode of life. P. deweyensis is distinguished from most species described from the Upper Cretaceous of the Western Interior and Gulf and Atlantic Coastal Plains by its suboval shape, prominent umbones and the number of plicae. Pholadomya subventricosa Meek & Hayden, coloradoensis Stanton, and tippana Conrad (= occidentalis Morton and conradi Gardner, fide Stephenson, 1955) differ by their elongated shape and 25 to 31 plicae. P. ironensis Stephenson, varicosta Stephenson, littlei Gabb and roemeri Whitfield are generally more elongated and have fewer costae (12-17). Several of the above species also grow to three to four times as large as deweyensis. P. deweyensis more closely resembles species described from the Upper Cretaceous of Canada. In shape it closely resembles maclearni Landes (1940, Pl. 4, figs. 6, 7), Lea Park Formation and upper Pakowki Shale (Campanian), but maclearni has about 25 not so widely spaced and finer plicae which become much weaker posteriorly, and is more inflated (1/2 W/L = 29.7%). Pholadomya cupressensis Landes (1940, Pl. 4, figs. 1-3), Eastend Formation (Maestrichtian) has 19 plicae, but even allowing for the distortion, it appears to have a more elongated subquadrangular shape (H/L = 41%) and a prominent narrow projecting anterior end. Pholadomya albertensis Warren (1933), Kaokapau Formation, Smoky River Group (Cenomanian-Turonian) is more elongated, the posterodorsal margin is concave and has about 20 plicae "confined" to the central part of the shell. It shows traces of radial plicae posterodorsally and is so poorly preserved that it should be considered specifically indeterminable.

The consistent shape and ornament, especially the number and nodose form of the plicae, of deweyensis are not matched by any of the Canadian species and, although larger samples are perhaps required to prove distinction from maclearni, the differences

coupled with the stratigraphic position justify a new name.

GONIOMYA

Author. Agassiz, 1842, p. 1.

Type Species. By subsequent designation of Herrmannsen (1846, p. 486), Mya angulifera J. Sowerby (1819, p. 46, Pl. 224, figs. 6, 7), Bathonian (Jurassic), England.

Goniomya americana Meek & Hayden (Plate 39, figs. 1–7)

Goniomya americana Meek & Hayden, 1856a, p. 81. Meek, 1876, p. 221, Pl. 30, figs. 12a,b. Pholadomya americana (Meek & Hayden). Gabb, 1861, p. 164.

Description. Large, specimens 14 to 79.5 mm long, equivalve, inequilateral. Umbones prominent, projecting, incurved, prosogyrous. Maximum inflation at about half the height, in posterior half of shell along the broad umbonal to posteroventral margin ridge. Height, half width, anterior length and length of nymph, respectively, 46.5 to 59.6 (N = 14, $\mu = 52.3\%$), 12.4 to 17.2 (N = 14, $\mu = 14.7\%$), 26.3 to 32.1 (N = 14, $\mu = 29.4\%$) and 10.5 to 15 (N = 8, $\mu = 12.4\%$) percent of length. Dorsal surface anterior to umbones is flat or weakly concave, bounded by sharp angulations (Pl. 39, fig. 5). Anterodorsal margin slightly concave, descends ventrally, anterior end rounded. Posterodorsal margin straight or concave when the posterodorsal extremity may extend dorsally, posterior end rounded. Ventral margin broadly convex, generally with one and sometimes two sinuses when broad low folds and furrows cross height of shell in vicinity of umbones. A slightly opisthoclinal umbonal to ventral margin plica sometimes strong. Umbonal to anteroventral plica indefinite to moderately distinct.

Shell ornamented with concentric striae and irregular plicae crossed by prominent V-shaped plicae, the axis of the V inclined prosoclinally and the posterior limb becoming asymmetric with increasing size and tending to form a gradual curve. Nineteen to 25 V-plicae on specimens 50 to 55 mm long. Anteriorly and posteriorly the limbs of the V's intersect the ventral margin and tend to be knotted by the concentric plicae.

Hinge narrow, edentulous, with vague undulations under umbone and anterior end of nymph. Nymph short, strong, bears an external opisthodetic ligament. Adductor insertion areas weakly impressed, sited in dorsal three eighths of height, subequal. Anterior adductor slightly smaller, subelliptical and attenuated dorsally, separated by a small gap from a small oval impression (pedal retractor). Posterior adductor subrectangular with a narrow dorsal prolongation. Pallial line relatively wide, with a very shallow asymmetric sinus in ventral two thirds of limb below posterior adductor (YPM 24148).

Ostracum thin, up to 0.3 mm thick over main disc, of two layers. A thin outer translucent homogeneous or prismatic layer and an inner pearly lamellar layer about three times thicker.

Types. Lectotype of Goniomya americana, USNM 432, by subsequent designation of Meek (1876, in caption to Pl. 30, fig. 12a), not located. Type locality: Moreau River, South Dakota. Stratigraphic position: Fox Hills Formation, probably from the Timber Lake Member.

Hypotypes YPM 24145-50 are held at YPM.

Discussion. The fine granules on the outer shell surface observed by Meek were seen on only one specimen (YPM 24150), primarily because the outer shell is poorly preserved. The granules are arranged semiregularly or in rows, and may be the external reflection of punctae in the outer shell layer.

MATERIAL. 85 specimens as steinkerns and with inner shell.

Occurrence. A relatively uncommon species. Twenty-six of the specimens came from the Timber Lake Member along the Moreau River. All but five of the remainder were collected from the Lower *nicolleti* Assemblage Zone (64.7%). The valves of most specimens although displaced are associated. Single valves are more common in the Lower *nicolleti* Assemblage Zone. Only two concretions contained more than one specimen, one provided seven and the other two.

Specimens from the Lower nicolleti Assemblage Zone do not exceed 30 mm in length whereas those from the Timber Lake Member are more than 38 mm long. The prevalence of articulated specimens and their preservation in the Lower nicolleti Assemblage Zone indicate that some were living approximately in place. The size differences may be due to chance preservation and recovery, or to juvenile substrate preferences or tolerances.

COMPARISON. No other species of *Goniomya* has been described from, and *americana* cannot be confused with any other species from the Upper Cretaceous of the Western Interior. The few records suggest that *americana* is uncommon.

POROMYACEA

CUSPIDARIA

Author. Nardo, 1840, p. 50.

Type Species. By monotypy, Tellina cuspidata Olivi (1792, p. 101), Recent, Mediterranean.

Cuspidaria moreauensis (Meek & Hayden) (Plate 39, figs. 8–16)

Corbula moreauensis Meek & Hayden, 1856a, p. 83.

Leda moreauensis (Meek & Hayden). Meek & Hayden, 1856c, p. 284.

Neaera moreauensis (Meek & Hayden). Meek & Hayden, 1860a, p. 185. Meek, 1876, p. 239, Pl. 17, figs. 11a-c. [?]Whitfield, 1880, p. 420, Pl. 11, fig. 31.

Cuspidaria moreauensis (Meek & Hayden). Kellum, 1962, p. 53.

Description. Small, specimens 4.4 to 8.4 mm long, inequilateral, slightly inequivalve, the relations of the valves as for *C. ventricosa* (p. 155), with maximum overlap of left valve along posterior half of ventral margin and the right valve overlapping only slightly in front of umbones. Anterior and ventral margins of right valve fit into a shallow narrow groove, which is bordered above by a relatively wide, low, round-topped costa and below by a weak costa. Umbones low, weakly prosogyrous or pointing centrally, almost touching, usually worn. Maximum height at umbones. Maximum inflation at about mid-height, below umbones, anterior end bulbuous, tapers rapidly posteriorly. Posterodorsal surface behind beaks concave, bordered by a raised umbonal to posterodorsal extremity costa below which is a second stronger raised costa extending from umbone to posteroventral point of rostrum. The latter costa sometimes weak posteriorly on rostrum. Rostrate, the rostrum moderately long and narrow, curving dorsally giving a concave dorsal margin.

Ends of rostrum flare outward producing a relatively prominent gape. Height, half width and anterior length of left valve, respectively, 57.3 to 64.5 (N = 13, μ = 61.1%), 20.8 to 25 (N = 12, μ = 23%) and 36.5 to 43.2 (N = 13, μ = 40%) percent of length. Same parameters for right valve, respectively, 55.8 to 65.9 (N = 24, μ = 59.8%), 17.3 to 25 (N = 23, μ = 21.7%) and 34.6 to 42.9 (N = 24, μ = 38.4%) percent of length. Shell ornamented with concentric striae and strong plicae, which are weak or strong on the interior of shell, of variable shape and pattern, mostly strong and sharp crested on umbones, sometimes weak and less regular ventrally, become weak and pass into striae on rostrum, although the costae and plicae extend posteriorly on rare specimens. Interspaces wider than plicae, may be marked by regular or irregular much weaker secondary costae.

Hinge morphology similar to *Cuspidaria ventricosa*, except that the left valve has the dorsal margin in front of the resilifer thickened and projecting to fit into a shallow socket under the overlapping margin of the right valve, and the right valve has a prominent projecting prosoclinal lamella extending subparallel to the dorsal margin for a short distance from above the posterior end of the posterior adductor insertion area. Musculation and pallial line as for *ventricosa*.

Ostracum up to 0.15 mm thick, of two layers apparently of the same structure as ventricosa.

Types. Lectotype of Corbula moreauensis, USNM 420, by subsequent designation of Meek (1876, in caption to Pl. 17, fig. 11a), a right valve, shell incomplete and missing posteriorly, L = 6.6, H = 4.2, 1/2 W = 1.3, AL = 1.9 mm. Type locality: Moreau River, South Dakota. Stratigraphic position: Fox Hills Formation. The lectotype is associated with *Phelopteria* in Timber Lake Member lithology.

Hypotypes YPM 24131-36, 24144, 24500 are held at YPM.

Discussion. Waage (1968) has described the known routes of Hayden's expeditions across the area of the type Fox Hills. He has thus explained the nondiscovery (Meek, 1876) in this region of many distinctive species common only in the Trail City Member.

Meek's description of *moreauensis* is an anomaly as it has been found here only below the *Protocardia-Oxytoma* Assemblage Zone, Trail City Member. The original specimens may represent an aberrant discovery higher in the section, perhaps in the muddy Irish Creek facies, or the collection of float specimens from traders and others.

The prominent lamella behind the posterior adductor muscle scar in the right valve is present on the smallest and largest specimens. It is weaker on a few valves but always considerably stronger than the weak protuberance in a similar position on some right valves of ventricosa. Functionally, the lamella probably strengthened the interlocking of the left valve and also aided the opening and closing of the ventral margin as part of the pumping action (Yonge, 1928). The systematic value of the lamella is uncertain. As ventricosa has a small protuberance it is considered here to be of species rank only.

MATERIAL. 328 specimens.

Occurrence. Virtually restricted to the Lower nicolleti Assemblage Zone (83.8%) where it is relatively uncommon. Forty-five (13.8%) specimens came from the overlying Limopsis-Pseudoptera Assemblage Zone. The species was found in 35 concretions at 25 localities, mainly as less than six specimens per concretion. Nine concretions provided more than 10 individuals. Four of these, where moreauensis is a codominant with Protocardia or Tenuiptera, contained more than 20, one having 44. Articulated valves (56.2%) dominated in most concretions.

Comparison. Poorly preserved specimens, especially when the plicae are weak on the shell interior, tend to resemble some individuals of ventricosa. Cuspidaria moreauensis is distinguished by its dorsally curving rostrum, and its two narrow projecting costae, lower height and inflation, more medially situated umbones, which are low and not so tumid, and the presence of strong plicae on the umbones, whereas ventricosa has only weak striae or fine irregular costae on the umbones. Internally, the presence of the strong lamella behind the posterior adductor of the right valve provides positive identification.

Cuspidaria ventricosa (Meek & Hayden) (Plate 40, figs. 1–9)

Corbula ventricosa Meek & Hayden, 1856a, p. 83.

Leda ventricosa (Meek & Hayden). Meek & Hayden, 1856c, p. 284.

Neaera ventricosa (Meek & Hayden). Meek & Hayden, 1860a, p. 185. Meek, 1876, p. 238, Pl. 30, figs. 3a-e.

[?] Cuspidaria ventricosa (Meek & Hayden). Weller, 1907, p. 533, Pl. 58, figs. 16-17. Richards, 1958, p. 172, Pl. 28, fig. 2.

Description. Small, specimens 4.6 to 12.3 mm long, inequilateral, slightly inequivalve, the dorsal margin of the left valve, especially the posterior, fitting under that of the right valve, narrow and projecting dorsally, and its anterodorsal, anterior and ventral margins projecting beyond those of the right valve and incurved. Anterior and ventral margins of right valve fit into a weak depression on the left valve. Umbones tumid, prominent, prosogyrous, almost touching, generally worn, and right valve umbone projects slightly higher. Maximum height and inflation as for *C. moreauensis*. Rostrate, the rostrum relatively short, the posterior dorsal margin straight. Posterior gape small. Height, half width and anterior length of left valve, respectively, 64.9 to 71.7 (N = 8, μ = 67.1%), 24.2 to 29.5 (N = 6, μ = 26.2%) and 28.6 to 34.1 (N = 8, μ = 31%) percent of length. Same parameters for the right valve, respectively, 63.7 to 71.4 (N = 11,

 $\mu=67.4\%$), 22.2 to 30.1 (N = 10, $\mu=26.3\%$) and 28.3 to 34.1 (N =11, $\mu=30.1\%$) percent of length. Shell ornamented by fine concentric striae and irregular costae, more raised and stronger above a weak ridge extending from behind umbone to posteroventral point of rostrum, and the costae strongest ventrally. A second weak sharp-crested ridge passes from tip of umbone to end of rostrum along the dorsal margin, strongest anteriorly.

Valves with a narrow deep prosoclinal resilifer under umbone, apparently opening to the exterior anterior to tip of umbone. Left valve edentulous, a shallow depression in dorsal margin in front of the resilifer aids matching with right valve. On the right valve a long strong projecting lamella (posterior tooth), its dorsal surface granular, parallels the posterior margin between resilifer and anterior end of adductor scar. Some valves show a weak linear prosoclinal protuberance behind the posterodorsal margin of the adductor scar. Adductor insertion areas subequal. Anterior smaller, weakly impressed, straddling mid-height close to anterior margin, elongate-elliptical, its posterior margin concave. An oval more deeply impressed insertion (anterior septal muscle insertion) is fused to its dorsal margin. Posterior adductor insertion deeply impressed, close to dorsal margin at base of rostrum, subtrapezoidal, with a small deeply impressed elliptical insertion (posterior septal muscle insertion area) above its mid-length and under the end of the lamellar tooth on the right valve. Below the hinge on either side of the umbonal cavity are small oval insertions (lateral septal muscles). Pallial sinus broad, shallow, asymmetric, forms a cusp where it joins ventral limb of the pallial line. Ends of pallial line join the anteroventral margins of the adductor insertion areas.

Ostracum up to 0.4 mm thick, of two layers. An outer concentric cross-lamellar layer, and an inner prismatic calcitic layer. Inner surface above pallial line with weak radial striae, strongest dorsally in umbonal cavity.

Types. Lectotype of *Corbula ventricosa*, USNM 419, by subsequent designation of Meek (1876, in caption to Pl. 30, fig. 3a), a bivalved specimen with some shell missing, L = 7.8, H = 4.8, W = 3.4, AL = 2.3 mm. Type locality: Moreau River, South Dakota. Stratigraphic position: Fox Hills Formation, probably from the Timber Lake Member.

Hypotypes YPM 24137–43, 24745 are held at YPM.

The original of figure 3c in the same collection (USNM 419) now has the central part of the hinge broken.

Discussion. The nomenclature of the muscle scars is based on Yonge (1928). The anterior septal muscle of living species does not appear to be fused to the anterior adductor muscle (Pelseneer, 1888, 1891; Grobben, 1893), nor is the posterior septal muscle sited so close to or above the center of the posterior adductor. These changes in position may have increased the efficiency of the pumping operation of the septum.

MATERIAL. 151 specimens.

Occurrence. A relatively rare but distinctive species that occurs mainly in the Timber Lake Member and its lateral equivalent of the Irish Creek lithofacies (57.4%), especially along the Moreau River where it was found in all assemblage zones. For stratigraphic distribution see Figure 4. Articulated valves dominated in the Lower *nicolleti* Assemblage Zone, and these probably lived in the vicinity. Single valves are more numerous in the other assemblage zones and may have been transported in.

The species was found at 19 localities, mostly as one or two specimens in 32 concretions. Three concretions contained seven and one (All80, Loc. 121) nine specimens.

Comparison. See above under *moreauensis* (Meek and Hayden). The specimens figured by Weller (1907) and Richards (1958) are too poorly preserved to identify positively.

RUDISTACEA

ICHTHYOSARCOLITES

Author. Desmarest, 1817, p. 51.

Type Species. Ichthyosarcolites triangularis Desmarest (1817, p. 51).

Ichthyosarcolites? sp. A (Plate 40, figs. 10–12)

Two fragmented but almost complete specimens were found in concretions at two localities in the *Protocardia-Oxytoma* Assemblage Zone. Caldwell and Evans (1963) have reviewed the rudistids recorded from the Upper Cretaceous of the Western Interior and tentatively placed them in *Ichthyosarcolites*. MacGillavry (1959) considers that this is an Old World genus. During a visit to Yale in March 1964, he examined the specimens from the type Fox Hills and considered (pers. comm.) them conspecific and best placed in a New World genus *Antillocaprina* aff. genus A (MacGillavry, 1937). As the status of *Antillocaprina* is uncertain (Caldwell and Evans, 1963), the Fox Hills specimens, which have a septate body chamber, are here tentatively placed in *Ichthyosarcolites*.

Description. The largest specimen is about 80 mm high and long, and about 50 mm wide. Cyrtoconic, the initial part tightly coiled, the distal cup greatly enlarged, oval in cross-section. Shell with three prominent projecting flanges on the convex side of cone, one on the bilateral axis and the others at about 70 degrees on either side. Body chamber on inside of cone, septate basally (YPM 24696). Outer wall composed of relatively regular hollow prisms whose long axis in tangential section is radial. Major part of shell consists of irregularly arranged hollow polygonal prisms up to 2 mm maximum width, divided by very thin, flat or concave, irregularly spaced diaphragms which do not cross the thicker prism walls.

Discussion. The fragmentation of the specimens and the discovery of only two specimens (YPM 24696, 24697) in the several thousand *Protocardia-Oxytoma* concretions dismembered emphasizes their rarity and indicates that in this region the rudistid was non-reef-forming. The larger specimen is almost twice the size of any previously recorded.

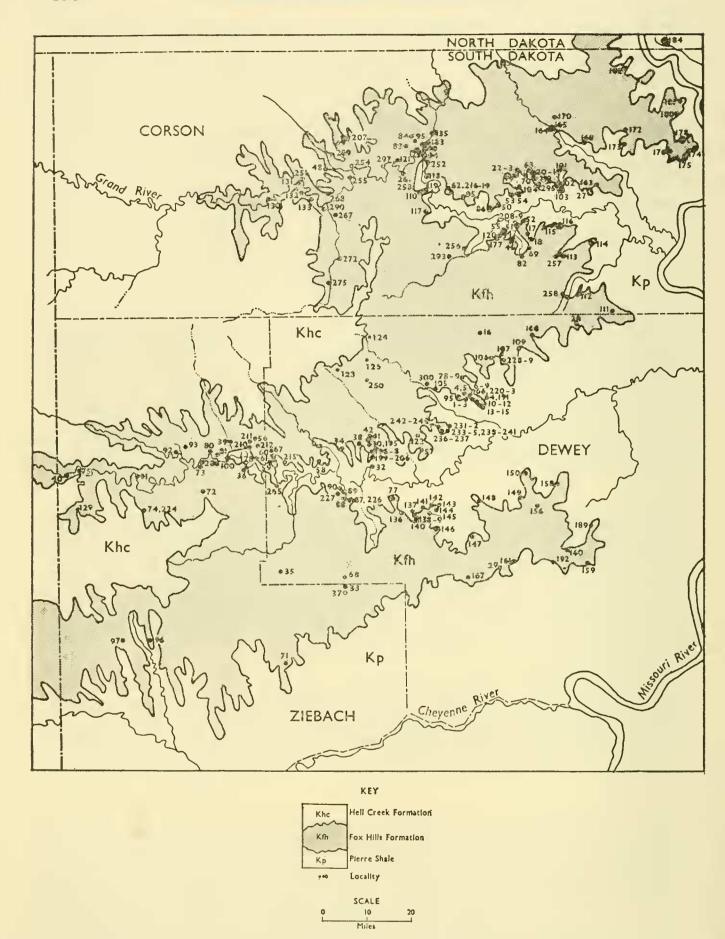


Fig. 19. Outcrop of the Fox Hills Formation in the type area showing the position of important fossil localities, including those mentioned in the text and illustrations, but excluding Loc. 44 (Seaman Park, Linton, North Dakota), Loc. 88 (Solen, North Dakota), and Locs. 185–187 (west of Pollock, North Dakota). (After Waage, 1968)

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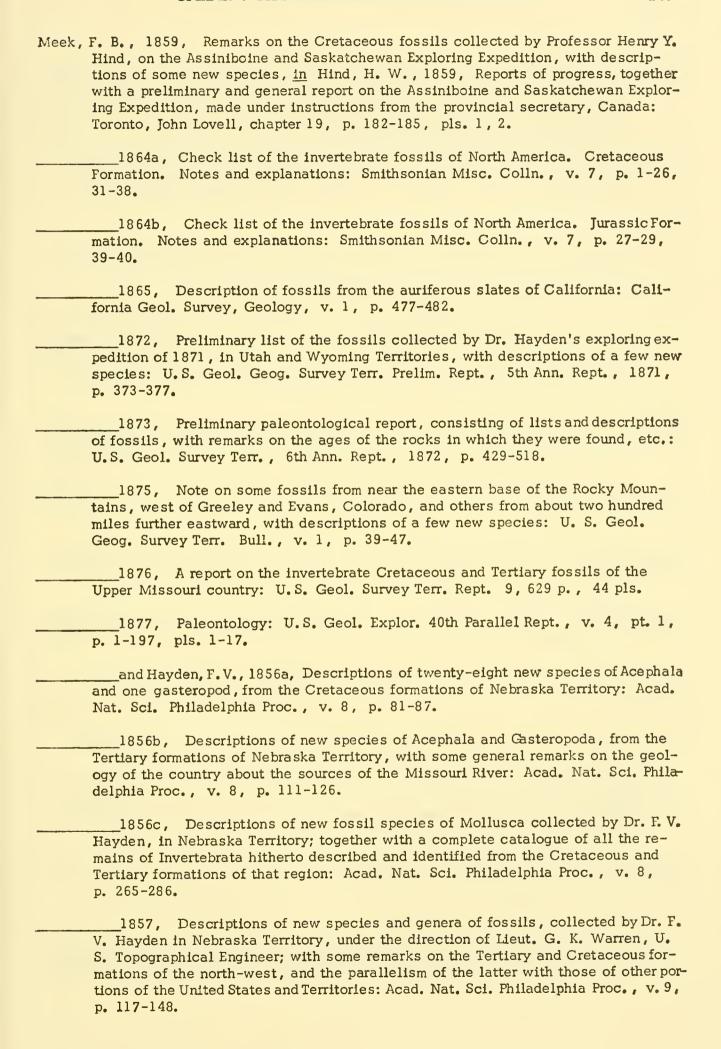
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APPENDIX BASIC STATISTICAL DATA

Coef. var.

l. Nucula cancellata					
Meek & Hayden					
(Equivalve)	Leng th	Height	Posterior length	Height of posterior angulation	Half width
N	78	78	78	7 8	77
Min.	4.100	3.000	1.400	1.600	1.000
Max.	24.600	18.300	9.000	11.400	7.400
Range	20.500	15.300	7.600	9.800	6.400
Mean	15.077	11.040	5.000	6.396	3.866
Std. dev.	6.166	4.601	2.133	2.716	1.814
Var.	38.019	21.167	4.549	7.378	3.292
Coef. var.	40.897	41.674	42.658	42.466	46.931
2. Nucula planomargi Meek & Hayden (Equivalve)	Inata				
		m a			
N	72	72	71	71	66
Min.	3.800	2.800	1.000	2.000	0.600
Max.	24.300	20.000	7.100	11.300	6.100
Range	20.500	17.200	6.100	9.300	5.500
Mean	9.982	7.494	2.973	4.550	1.882
Std. dev.	5.243	3.889	1.541	2.264	0.959
Var,	27.491	15.128	2.374	5.127	0.920
Coef. var.	52.527	51.898	51.821	49.764	50.969
3. Nucula percrassa Conrad (Equivalve)					
N	6	6	6	6	5
Min.	8.200	5.300	2.800	3.100	1.900
Max.	34.800	21.300	11.200	11.200	8.000
Range	26.600	16.000	8.400	8.100	6.100
Mean	19.050	12.233	6.450	6.600	4.260
Std. dev.	9.828	5.827	2.970	2.910	2.261
Var.	96.587	33.959	8.823	8.468	5.113

51.590 47.635 46.052 44.091

53.080

4. Nuculana (Nuculana) grandensis Speden (Equivalve)

	Length	Height	Anterior length	Half width
N	9	9	9	6
Min.	10.200	3.700	2.600	0.600
Max.	27.100	7.500	7.300	1.000
Range	16.900	3.800	4.700	0.400
Mean	17.089	5.433	4,467	0.783
Std. dev.	6.035	1.444	1,553	0.147
Var.	36.419	2.085	2.412	0.022
Coef. var.	35.314	26.576	34.774	18.791
5. <u>Nuculana</u> (Ju (Meek & Hay (Equivalve)				
N	134	134	134	134
Min.	2.800	2.000	1.300	0.500
Max.	10.600	6.100	4.200	2.400
Range	7.800	4.100	2.900	1.900
Mean	6.662	3.969	2.666	1.285
Std. dev.	1.577	0.911	0.621	0.447
Var.	2.486	0.830	0.385	0.200
Coef. var.	23.665	22.947	23.285	34.794
6. <u>Yoldia lacrin</u> Speden (Equivalve)	<u>na</u>			
N	8	8	8	7
Min.	5.000	2.500	2.100	0.200
Max.	24.000	9.500	9.200	0.900
Range	19.000	7.000	7.100	0.700
Mean	9.662	4.400	3.963	0.471
Std. dev.	6.474	2.459	2.454	0.325
Var.	41.908	6.046	6.020	0.106
Coef. var.	66.998	55.882	61.919	68.969

Coef. var.

56.773

7. <u>Yoldia recta</u> Speden (Equivalve)	ngularis_			
	Length	Height	Anterior length	Half Width
N	5	5	5	5
Min.	6.600	3.100	2.100	0.300
Max.	19.100	8.000	6.400	1.200
Range	12.500	4.900	4.300	0.900
Mean	14.840	6.620	5.120	0.820
Std. dev.	4.938	2.041	1.768	0.335
Var.	24.383	4.167	3.127	0.112
Coef. var.	33.274	30.836	34.538	40.813
8. <u>Malletia eva</u> (Meek & Ha (Equivalve)				
N	98	98	98	98
Min.	3.600	2.200	1.100	0.300
Max.	18.500	7.800	5.800	2.400
Range	14.900	5.600	4.700	2.100
Mean	11.146	5.427	3.965	1.178
Std. dev.	3.048	1.305	0.977	0.459
Var.	9.288	1.704	0.954	0.211
Coef. var.	27.342	24.054	24.627	38.993
9. <u>Solemya</u> <u>sub</u> (Meek & Ha (Equivalve)			Posterior length	
N	7	7	7	5
Min.	7.300	3.100	1.200	1.000
Max.	38.000	16.800	7.200	4.200
Range	30.700	13.700	6.000	3.200
Mean	20.771	8.357	3.671	2.500
Std. dev.	11.792	5.044	2.410	1.311
Var.	139.062	25.443	5.806	1.720

60.357

65.629

52.460

10. Limopsis striatopunctatus Evans & Shumard (Equivalve)

	Length	Height	Anterior length	Half	Length of cardinal area	Anterior length of cardinal area	Length of Ilgament pit	Length of hinge	Number of Teeth anterior post	of Teeth posterior
Z	400	399	400	399	309	310	31	25	26	26
Min.	3.100	2.900	1.000	0.800	1.700	0.700	0.600	4.600	7,000	7.000
Max.	18.600	16.600	7,400	5.500	8.000	3.800	3,500	9,800	10.000	12,000
Range	15,500	13,700	6.400	4.700	6.300	3,100	2,900	5,200	3,000	5,000
Mean	9.837	8,547	3,495	2,831	4,466	1.697	1,419	6, 412	8,192	9, 423
Std. dev.	3,330	2,734	1.111	1.014	1.343	0.526	0.796	1,395	0,749	1.238
Var.	11.089	7,473	1,233	1.027	1.804	0.277	0.634	1.945	0.562	1.534
Coef. var.	33,851	31,984 31,773	31,773	35,799	30.078	31,011	56.082	21.752	9.147	13,143

	Width (both valves)	54	3.000	62.000	29,000	16.581	10.876	118,285	65.591	Number of ligament grooves* left right	70	1.000	11,000	10,000	4,150	2,091	4.372	50,385
	width right	105	1.300	31,000	29,700	7.617	5,745	33,000	75.416	Number of ligament groo left ris	52	1.500	11.000	9.500	4.200	1,750	3.061	41.657
	Half v	98	1.200	31,000	29,800	7,344	5, 235	27,408	71.288	Length of hinge line ft right	16	3.100	44.600	41.500	15.050	12,339	152,239	81,983
ulvalve)	length right	105	1.600	28,200	26.600	9,549	6.158	37,926	64,496	Leng hing left	11	3,500	37,500	34,000	13,518	10,576	111,862	78.239
Owen (Inequivalve)	Anterior left	26	1.600	26.800	25.200	9,390	5.824	33,919	62,025	Width of cardinal area sft right	81	0.200	7.300	7,100	1,414	1.254	1.572	88,702
Cucullaea nebrascensis	right	106	3,500	63.600	60.100	19,506	12,853	165,195	65.893	Wid cardin left	59	0.200	5,100	4,900	1.403	0.973	0,946	69,300
Cucullaea n	Height left r	96	3.500							Length of urdinal area t right	95	1,300	44.700	43,400	11,865	8,962	80,313	75, 529
11.		0,		0 64.700	0 61.200	19,300	5 12.617	9 159,198	5 65,375	Length of cardinal are left	73	1.200	42,100	40,900	12,041	8,176	66,853	67.904
	Length right	106	4,300	71,300	67,000	21.874	13,926	193,929	63, 665	h of nargin right	106	2,600	47.500	44,900	14.541	10,117	102.356	69, 578
	left	97	3,800	72,700	68,900	21,662	13,496	182,149	62,304	Length of dorsal margin left righ	95	2,500	45.700	43.200	14,215	9.846	96.946	69, 267
		Z	Min.	Max.	Range	Mean	Std. dev.	Var.	Coef. var.		Z	Min.	Max.	Range	Mean	Std. dev.	Var.	Coef. var

* Fractions result from averaging the number of grooves on the anterior and posterior segments of the ligament area. 0.5 indicates that one segment had one groove more, or less, than the other.

			12.	Cucullaea	Cucullaea wadel Imlay		(Inequivalve)			
	Len left	Length right	left	Helght right	Ant left	Anterior length sft	ngth right	Half width left	idth right	Width (both valves)
Z	33	24	33	24	33		24	က	24	ω
Min.	42,800	45,400	37,700	40.200	19,600		21.000	14,200	13,800	45,600
Max.	80,300	81,200	76,900	76.800	37,700	00,	40.200	36,700	40.500	000 *69
Range	37,500	35.800	39,200	36,600	18,100	00	19,200	22,500	26.700	23,400
Mean	67,127	67.749	60,542	62,171	30,800	008	31.392	26,639	27.733	54,762
Std. dev.	10.383	8.434	10,229	9.070	4,526	126	4.057	6,134	5,939	9,082
Var.	107,810	71.126	104.638	82,262	20,481	181	16.460	37,631	35,273	82,486
Coef. var.	15,468	12,498	16,896	14,589	14,694	94	12,924	23.027	21,415	16,585
	Length of dorsal margin left righ	th of margin right	Length cardinal left	h of 1 area right	Width of cardinal area left rigl	n of 1 area right	Lengham hing left	Length of hinge line ft right	Num Ilgamer left	Number of Ilgament grooves left right
z	33	24	32	24	ဗ	23	31	18	ლ	61
Min.	10.400	27, 400	21,800	23,700	1,200	2,400	28.500	35,300	3,000	3,000
Max.	51,400	56.900	48.000	55,000	8.800	11,000	52,500	56.000	11.000	9,000
Range	41,000	29, 500	26.200	31,300	7.600	8.600	24,000	20,700	8,000	6.000
Mean	40.282	42,246	38,550	39, 996	3,979	5.057	42,471	43,822	5,032	5.868
Std. dev.	8.094	5.892	7,154	6,920	1.789	2,317	6.470	5,274	1,919	1,978
Var	65, 508	34,715	51,179	47,882	3,200	5.367	41.863	27,814	3, 682	3,912
Coef. var.	20,093	13,947	18,558	17,301	44,963	45,816	15,234	12,035	38,132	33, 705

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(Cosmetodon)
Parallelodon
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Width (both valves)	22	1.900	6,500	4.600	3,845	1,416	2,006	36,835	Number of ligament grooves if	15	1.000	3.000	2,000	2,000	0.845	0.714	42,258
Half width right	41	0.800	4.200	3,400	2,017	0.732	0.536	36,311	Nu: 11gam 1eft	17	1.000	5,000	4.000	2,529	1.068	1.140	42,206
Hali left	43	0.600	3,700	3,100	2,100	0.704	0,496	33,543	r of costae right	0	-1.000	-1.000	-1.000	000.0	000.0	00000	-1.000
Anterior length eft right	40	1.400	5.000	3,600	2.790	0.854	0.730	30,627	Number of secondary costae left	Н	56,000	56.000	0.000	000.0	0.000	00000	-1.000
Anteric left	51	006 0	5.000	4,100	2,937	0,955	0,912	32,520	ae right	23	21.000	32,000	11.000	25.913	3.161	9,992	12.199
tright	50	2.500	8.000	5.500	5,512	1.425	2.031	25.854	Number of primary costae	2				25			12
Height left	56	1.800	8.600	6.800	5,957	1.557	2,424	26,135	pri	21	20.000	30,000	10,000	24,381	2,459	6.048	10.087
th right	49	4.600	14.400	9.800	9,477	2,566	6,583	27.160	Length of dorsal margin right	41	4.100	13,800	9,700	8.444	2,453	6.020	29,056
Length left	55	2.800	15,600	12,800	9.900	2, 788	7,770	28,157	Leng dorsal left	51	2,500	13,800	11.300	8,647	2,363	5,585	27,331
	Z	Min.	Max.	Range	Mean	Std. dev.	Var.	Coef. var.		Z	Min.	Max.	Range	Mean	Std. dev.	Var.	Coef, var.

14. Pseudoptera subtortuosa (Meek & Hayden) (Inequivalve)

							Leng	Length of			
	Leı	Length	Height	ght	Obliqu	Oblique length	ligame	ligament area	Hall	Halfwidth	Width
	left	right	left	right	left	right	left	right	left	right ((both valves)
Z	43	65	43	65	43	65	42	64	42	49	25
Min.	5.100	3.900	4.000	3.100	5.800	4.100	4.400	3,500	0.400	0.300	1.700
Max.	92.800	122.700	56.300	72.800	105.500	126.400	29,000	78.700	7.200	12,600	11,400
Range	87.700	118.800	52.300	69.700	99.700	122.300	54.600	75.200	6.800	12,300	9.700
Mean	30.607	34.026	23.751	25.018	35.407	38.963	17.660	22.003	3.307	2, 286	5.160
Std. dev.	18,176	24.073	11.701	14.660	20.399	25.712	11.901	15.992	1.579	2,396	2.272
Var.	330,361	579.517	136,914	214.914	416.137	661,130	141.630	253.506	2,493	5.740	5.160
Coef. var.	59,385	70,749	49,265	58.597	57,614	65.992	67.391	72.362	47.746	104,821	44.023

15. Phelopteria linguaeformis (Evans & Shumard) (Inequivalve)

	Leng	gth	Heig	ght	Anterio	length
	left	right	left	right	left	right
N	35	34	31	37	30	37
Min.	6.200	3.900	5.100	2.900	1.500	1.300
Max.	62.400	50.900	50.500	41.600	11.500	11.400
Range	56.200	47.000	45.400	38.700	10.000	10.100
Mean	21.589	18.741	18.484	13.992	4.870	4.689
Std. dev.	14.510	11.889	11.804	8.759	2.388	2.633
Var.	210.531	141.343	139.332	76.724	5.705	6.932
Coef. Var.	67.210	63.437	63.861	62.602	49.045	56.146

			Leng	gth of		
	Oblique	e length	ligame	ent area		width
	left	right	left	right	left	right
N	32	37	4	11	32	30
Min.	7.100	4.200	6.200	4.200	1.000	0.400
Max.	71.500	60.900	28.100	24.100	7.500	6.900
Range	64.400	56.700	21.900	19.900	6.500	6.500
Mean	26.288	20.370	15.575	14.618	3.097	2.400
Std. dev.	16.773	13.202	10.317	6.998	1.837	1.481
Var.	281.349	174.295	106.449	48.974	3.374	2.193
Coef. var.	63.808	64.811	66.243	47.873	59.312	61.705

	Width (both valves)	Length of poste		Prosocl (in deg left	_
N	7	30	36	29	30
Min.	2.000	5.500	3.500	31.000	33.000
Max.	10.000	35.000	43.900	49.000	50.000
Range	8.000	29.500	40.400	18.000	17.000
Mean	6.157	16.137	14.789	39.931	41.433
Std. dev.	3.376	7.962	9.023	4.488	4.321
Var.	11.396	63.397	81.407	20.138	18.668
Coef. var.	54.828	49.342	61.009	11.238	10.428

16. Oxytoma (Hypoxytoma) nebrascana (Evans & Shumard) (Inequivalve)

ength right	20	5.100	17.900	12.800	10.560	3.021	9,126	28.607	Prosoclinality (in degrees) ft right	16	38.000	51.000	13.000	44,750	2.978	8.867	6. 654
Oblique length left righ	48	4.500	30.200	25.700	15,890	5,589	31.241	35,176	Prosoclinallt (in degrees) left	42	32,000	42.000	10.000	37,905	2.438	5.942	6. 431
yth right	20	1.200	4.800	3.600	2,685	0.820	0.672	30,528	Number of costae eft	14	67.000	113,000	46.000	86.571	13.821	191,033	15,965
Anterior length left ris	48	1.100	6.100	5.000	3.050	0.877	0.769	28.750	Number left	œ	37,000	48.000	11,000	41.250	3.284	10,786	7.962
	6	4.000			8,895		6.610		Width (both valves)	0	-1.000	-1.000	-1.000	000 0	0.000	00000	-1.000
Height right	20	4. (14,300	10.300	8	2.571	6. (28,904	th right	13	009 0	006 6	9,300	1,646	2,495	6,224	151.557
Hed left	48	4.100	26.200	22.100	13.006	4.699	22.081	36.129	Half width left	38	0.600	3,000	2,400	1,550	0.613	0.376	39,536
th right	20	4.000	15.500	11.500	9,205	2,781	7.736	30.216	of area right	20	5.600	17.600	12,000	10.600	2,944	8,665	27.771
Length left	48	4.200	29.600	25.400	14.579	5,437	29,556	37.290	Length of ligament area left	48	3,300	19,100	15.800	10.700	3,553	12.627	33,210
	z	Min.	Max.	Range	Mean	Std. dev.	Var.	Coef. var.		Z	Min.	Max.	Range	Mean	Std. dev.	Var.	Coef. var.

Coef. var.

24.772

Length of ligament

25 0.500 5.900 5.400 2.868 1.939 3.758 67.594

17. <u>Crenella elegantula</u>
Meek & Hayden
(Equivalve)

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	Length	Height	Half width	Anterior length
N	83	83	83	77
Min.	1.800	1.600	0.500	0.100
Max.	24.600	16.500	7.900	1.700
Range	22.800	14.900	7.400	1.600
Mean	10.593	7.516	3.208	0.660
Std. dev.	6.845	3.961	2.250	0.533
Var.	46.856	15.692	5.064	0.284
Coef. var.	64.621	52.708	70.139	80.742
18. <u>Modiolu</u> (Evans & (Equival	Shumard)			
N	36	36	36	35
Min.	4.900	2.800	1.000	0.400
Max.	28.300	15.700	6.300	2.400
Range	23.400	12.900	5.300	2.000
Mean	13.744	7.597	2.575	1.494
Std. dev.	4.340	2.211	0.960	0.477
Var.	18.835	4.887	0.921	0.228
Coef. var.	31.576	29.097	37.277	31.928
	s galpinianus Shumard) ve)			
N	10	10	10	10
Min.	15.300	8.500	2.300	0.700
Max.	37.100	20.100	6.500	3.700
Range	21.800	11.600	4.200	3.000
Mean	28.520	14.520	4.830	1.990
Std. dev.	7.065	3.266	1.451	1.148
Var.	49.915	10.666	2.107	1.319

22.493 30.051

57.708

20. Syncyclonema halli (Gabb) (Subequivalve)

	L ength	Height	Half width	Length of dorsal margin	Length of anterior dorsal margin	Anterior length	Opistho- clinality (indegrees)
N	27	27	25	18	19	27	21
Min.	4.000	4.000	0.200	2.500	1.300	1.700	87.000
Max.	13.200	14.400	1.200	5.800	3.600	6.700	100.000
Range	9.200	10.400	1.000	3.300	2.300	5.000	13.000
Mean	7.400	8.063	0.624	4.128	2.274	3.578	92.095
Std. dev.	2.352	2.607	0.211	0.921	0.618	1.165	3.767
Var.	5.530	6.799	0.044	0.848	0.382	1.356	14.190
Coef. var.	31.778	32.338	33.768	22.309	27.185	32.552	4.090

21. Anomia gryphorhyncha Meek (Inequivalve; data for left valve only)

	Length	Height	Half Width	Anterior length
N	35	35	34	9
Min.	2.300	2.400	0.2	0.400
Max.	26.200	29.600	10.100	2.200
Range	23.900	27.200	9.900	1.800
Mean	14.474	14.834	2.679	1.178
Std. dev.	7.965	8.528	2.396	0. 593
Var.	63.445	72.729	5.740	0.352
Coef. var.	55.030	57.489	89.420	50. 370

22. <u>Crassostrea subtrigonalis</u> (Evans & Shumard) (Inequivalve)

	Len	gth	He	lght
	left	right	left	right
N	57	20	57	20
Min.	4.800	24.600	6.400	35.200
Max.	77. 90 0	63.800	102.200	88.200
Range	73.100	39.200	95.800	53.000
Mean	36.253	38.055	54.812	60.975
Std. dev.	16.766	10.213	24.797	14.679
Var.	281.090	104.308	614.889	215.468
Coef. var.	46.247	26.838	45.240	24.074

	Half width		Width	Length of 1	igament pit
	left	right	(both valves)	left	right
N	49	20	1	56	19
Min.	2.800	2.600	24.900	1.300	7.600
Max.	25.100	8.800	24.900	24.600	26.600
Range	22.300	6.200	0.000	23.300	19.000
Mean	12.386	5.700	0.000	12.212	13.437
Std. dev.	5.081	1.754	0.000	6.057	5.859
Var.	25.820	3.076	0.000	36.689	34.328
Coef. var.	41.026	30.768	-1.000	49.598	43.604

	-	ht of ent pit	Distance of base of muscle scar below ligament		
	left	right	left	right	
N	56	19	46	18	
Min.	0.600	2.700	5.600	11.200	
Max.	20.900	12.400	36.000	30.600	
Range	20.300	9.700	30.400	19.400	
Mean	8.554	6.879	20.187	21.439	
Std. dev.	4.779	2.989	6.806	5.714	
Var.	22.836	8.932	46.322	32.647	
Coef. var.	55.868	43.446	33.715	26.651	

23. Ostrea translucida Meek & Hayden (Inequivalve)
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	Length			Height	
	left	right	left	right	
N	37	47	37	47	
Min.	9.800	5.800	12.600	6.100	
Max.	38.700	30.300	37.800	30.600	
Range	28.900	24.500	25.200	24.500	
Mean	22.086	16.815	24.459	18.889	
Std. de	v. 5.984	5.728	6.385	6.818	
Var.	35.806	32.809	40.771	46.490	
Coef.	var. 27.093	34.065	26.105	36.096	

	Half wi	d th	Width	Length of li	Length of ligament area	
	left	right	(both valves)	left	right	
N	36	44	7	31	39	
Min.	2.100	0.400	4.200	3.100	0.800	
Max.	8.400	4.900	7.100	9.900	7.200	
Range	6.300	4.500	2.900	6.800	6.400	
Mean	5.378	2.423	5.371	5.761	4.036	
Std. dev.	1.614	1.210	1.129	1.590	1.477	
Var.	2.605	1.463	1.276	2.528	2.182	
Coef. var.	30.010	49.928	21.027	27.596	36.599	

	Height of li left	igament area right	Distance of t scar below left	op of muscle w ligament right
N	31	39	14	35
Min.	1.300	0.200	8.400	2.800
Max.	5.000	3.500	19.000	14.400
Range	3.700	3.300	10.600	11.600
Mean	2.758	1.613	12.207	7. 69 7
Std. dev.	0.952	0.833	3.169	2.983
Var.	0.906	0.694	10.041	8.896
Coef. var.	34.508	51.645	25.958	38.749

24. <u>Corbicula</u> sp. A (Equivalve)

	Length	Height	Half width	Anterior length	Length of nymph
N	103	103	103	103	83
Min.	4.500	3.300	0.800	1.800	0.800
Max.	37.100	31.600	12.100	17.300	10.200
Range	32.600	28.300	11.300	15.500	9.400
Mean	20.101	17.187	5.824	7.785	4.300
Std. dev.	5.909	5.469	2.432	2.598	1.712
Var.	34.915	29.914	5.915	6.750	2.932
Coef. var.	29.396	31.822	41.758	33.372	39.821

25. <u>Spaniorinus nicolleti</u> Speden (Equivalve)

N	44	44	42	44
Min.	3.900	3.000	0.500	2.100
Max.	12.600	9.500	2.000	6.300
Range	8.700	6.500	1.500	4.200
Mean	9.552	7.025	1.202	4.986
Std. dev.	1.960	1.385	0.312	0.974
Var.	3.843	1.918	0.097	0.948
Coef. var.	20.522	19.713	25.944	19.523

26. <u>Hindsiella corsonensis</u> Speden (Equivalve)

N	13	13	12	13
Min.	5.200	3.800	0.800	2.300
Max.	8.800	6.100	1.700	4.000
Range	3.600	2.300	0.900	1.700
Mean	6. 68 5	4.723	1.142	3.038
Std. dev.	1.057	0.7 38	0.254	0.466
Var.	1.118	0.545	0.064	0.218
Coef. var.	15.818	15.634	22.240	15.351

27. Nymphalucina occidentalis (Morton) (Equivalve)

	Length	Height	Half width	Anterior length	Length of escutcheon	Height of anteroventral truncation above base
N	70	70	70	69	50	31
Min.	2.600	2.300	0.600	1.000	3.200	2.000
Max.	46.100	40.600	10.800	19.700	22.300	17.600
Range	43.500	38.300	10.200	18.700	19.100	15.600
Mean	30.071	25.719	6.343	12.275	15.528	10,642
Std. dev.	12.787	10.990	2.875	5.245	5.157	5.044
Var.	163.520	120.789	8.265	27.513	26.596	25.443
Coef. var.	42.524	42.733	45.324	42.730	33.212	47.399

28. <u>Clisocolus moreauensis</u> (Meek & Hayden) (Equivalve)

	Length	Height	Half width	Anterior length
N	45	45	45	44
Min.	3.200	2.900	1.100	1.400
Max.	46.300	43.800	17.200	18.700
Range	43.100	40,900	16.100	17.300
Mean	30.664	29.962	10.936	12.589
Std. dev.	15.549	15.195	5.725	6.432
Var.	241.772	230.881	32.778	41.364
Coef. var.	50.707	50.713	52.354	51.090

29. Tancredia americana (Meek & Hayden) (Equivalve)

12.894	2.873	1.726	18,650	7.151	31.281	61.789	Var.
3,591	1.695	1,314	4.319	2.674	5,593	7.861	Std. dev.
20.007	9, 605	6.789	21,452	11.234	30,335	41.868	Mean
23.100	11.200	8,400	24.900	15,900	35,300	48,300	Range
30.500	13.800	10.200	31.400	18.600	44.000	61.800	Max.
7.400	2.600	1.800	6.500	2.700	8.700	13,500	Min.
130	112	107	132	132	132	132	Z
Height of posteroventra angulation	DPLT*	Length of nymph	Anterior length	Half	Height	Length	

* DPLT=distance from umbone to posterior end of posterior lateral tooth.

23,000 2,689 7, 233 No. of costae 12,000 11,000 17,233 15,606 Length of nymph 0.00 1.700 1.100 1,155 0.218 18,849 0.047 22 Length of hinge line 5.100 2.500 4.210 0.526 2,600 0.277 12.501 Protocardia subquadrata (Evans & Shumard) (Equivalve) escutcheon 1.786 Length of 0.500 4.600 0.944 54,399 5.100 0.971 210 6.700 0.700 7.400 2,402 1,151 1.324 47.894 Half 336 1.200 11,900 3,482 1.558 10,700 2,427 Anterior length 338 Height 20.800 7.345 2.800 23,600 3,207 10,283 43,659 338 30. 24.800 21.800 11,365 3,000 7.888 42,738 Length 3,371 360 Coef. var. Std. dev. Range Mean Max. Min. Var.

31.	Protocardia
	sp. A
	(Equivalve)

fedutag	146)		Half	Anterior	375	Towards of
	Length	Height	width	length	No. of costae	Length of escutcheon
N	6	6	6	6	2	
Min.	52.500	48.000	17.500	17.200	26.000	
Max.	63.000	57.900	20.100	21.500	28.000	
Range	10.500	9.900	2.600	4.300	2.000	
Mean	56.383	54.350	18.817	19.650	27.000	
Std. dev.	3.947	3.650	1.026	1.803	1.414	
Var.	15.578	13.323	1.054	3.251	2.000	
Coef. var.	7.000	6.716	5.455	9.176	5.238	

32. <u>Dosiniopsis deweyi</u> (Meek & Hayden) (Equivalve)

N	90	90	90	90	54
Min.	7.600	6.800	1.500	3.300	4.800
·Max.	40.300	37.800	9.400	15.000	15.200
Range	32.700	31.000	7.900	11.700	10.400
Mean	25.101	22.786	6.122	9.602	9.102
Std. dev.	5.862	5.583	1.596	2.231	2.395
Var.	34.366	31.167	2.546	4.976	5.736
Coef. var.	23.355	24.501	26.064	23.231	26.314

33. Cymbophora warrenana (Meek & Hayden) (Equivalve)

N	60	60	60	60
Min.	3.300	2.800	0.900	1.400
Max.	46.200	38.000	12.300	18.200
Range	42.900	35.200	11.400	16.800
Mean	27.705	22.522	7.142	10.158
Std. dev.	12.354	9.877	3.163	4.510
Var.	152.618	97.553	10.007	20.341
Coef. var.	44.591	43.855	44.294	44.399

34. <u>Tellinimera scitula</u> (Meek & Hayden) (Equivalve)

	Length	Heigh t	Half width	Anterior length	Length of nymph
N	92	92	90	92	41
Min.	4.200	2.400	0.400	2.200	0.700
Max.	26.800	16.200	2.800	14.200	4.800
Range	22.600	13.800	2.400	12.000	4.100
Mean	16.641	9.523	1.321	8.889	2.602
Std. dev.	5.396	3.164	0.600	2.850	1.258
Var.	29.118	10.009	0.360	8.123	1.582
Coef. var.	32.426	33.223	45.437	32.063	48.327

35. Sourimis equilateralis (Meek & Hayden) (Equivalve)

N	14	14	14	14	8
Min.	23.000	14.500	2.700	10.500	4.600
Max.	51.400	34.200	9.900	24.600	13.500
Range	28.400	19.700	7.200	14.100	8.900
Mean	42.936	28.636	6.714	20.600	10.712
Std. dev.	9.806	7.260	2.274	4.863	3.381
Var.	96.156	52.715	5.169	23.646	11.430
Coef. var.	22.839	25.355	33.861	23.605	31.559

36. <u>Hiatella?</u> sp. (Equivalve)

N	4	4	4	4
Min.	9.500	5.800	2.100	3.500
Max.	24.000	12.800	4.000	7.200
Range	14.500	7.000	1.900	3.700
Mean	14.575	8.350	2.800	5.050
Std. dev.	6.722	3.214	0.876	1.733
Var.	45.189	10.330	0.767	3.003
Coef. var.	46.122	38.491	31.271	34.317

37. <u>Panopea occidentalis</u>
Meek & Hayden
(Equivalve)

	Length	Height	Half width	Anterior length	Length of nymph	Height at umbone
N	4	4	4	4	2	
Min.	31.500	18.000	4.500	14.000	14.000	
Max.	93.500	57.000	14.000	43.000	17.000	
Range	62.000	39.000	9.500	29.000	3.000	
Mean	76.375	46.325	11.250	35.325	15.500	
Std. dev.	29.956	18.916	4.518	14.225	2.121	
Var.	897.356	357.823	20.417	202.356	4.500	
Coef. var.	39.222	40.834	40.164	40.269	13.686	

38. <u>Cyrtodaria minuta</u> Speden (Equivalve)

N	12	12	12	12	12
Min.	6.500	3.600	0.400	2.000	3.200
Max.	12.000	6.500	1.100	3.800	6.000
Range	5.500	2.900	0.700	1.800	2.800
.Mean	8.583	4.517	0.717	2.717	4.125
Std. dev.	1.879	0.924	0.212	0.561	0.858
Var.	3.529	0.854	0.045	0.314	0.737
Coef. var.	21.886	20.463	29.650	20.635	20.806

		39.	Varicorbula crassimarginata (Meek & Hayden) (Inequivalve)	Imarginata	(Meek & Hayde	n) (Inequival	(ve)		
	left	Length right	Helght left	jht right	Half width left r	oldth right	Width (both valves)	Anterior left	Anterior length eft right
N	13	თ	4	10	15	14	Ø	14	თ
Min.	4,100	4.500	2.800	3,200	006 0	1.100	2,000	1.500	1.600
Max.	6,300	7.100	4.500	5,200	1.700	I.800	3,000	2,500	2.800
Range	2,200	2,600	1.700	2,000	0.800	0.200	1,000	1.000	1.200
Mean	5,100	6.200	3.679	4,450	1.260	1,398	2,400	2.043	2.400
Std. dev.	0.714	0.843	0.451	0.593	0.244	0.250	0,312	0.290	0.361
Var.	0.510	0.710	0.203	0.352	090.0	0.062	860 0	0.084	0.130
Coef. var.	14,003	13,591	12,259	13,326	19.394	17,913	13.010	14.202	15.023

(Meek & Hayden) (Inequivalve) Corbulamella gregaria 40.

	Length left	right	Height left	right	Half width left ri	ght	Width (both valves)	Anterior length left right	length right
×	71	10	70	69	69	73	29	69	19
Min.	1,600	2,400	1.400	1,600	0.500	0.600	1.000	0.700	1.000
Max.	3,400	3,300	3.200	3,500	1,300	1.500	2.800	1.600	1.500
Range	1,800	0.900	1.800	1.900	0.800	0.900	1.800	006.0	0.500
Mean	2, 568	2,853	2.341	2, 659	0.919	1.081	1.967	1.197	1.274
Std. dev.	0,355	0.284	0.332	0.330	0.168	0.180	0.359	0.176	0.152
Var.	0.126	0.080	0.110	0.109	0.028	0.032	0.129	0.031	0.023
Coef. var.	13.821	9,940	14.184 1	12, 426	18,314	16.655	18,251	14.678	11.948

* Only complete specimens measured.

^{**} Includes 50 specimens for which the height could be measured only from the ventral margin of the left valve. The projecting portion of the ventral margin had been broken off.

41. Opertochasma cuneatum (Meek & Hayden) (Equivalve)

	Length	Height	Half width	Anterior length	Number of costae
N	47	47	47	47	
Min.	6.400	3.200	1.200	0.700	
Max.	16.400	6.900	3.300	2.800	
Range	10.000	3.700	2.100	2.100	
Mean	10.387	4.555	2.074	1.519	
Std. dev.	2.547	0.890	0.409	0.404	
Var.	6.486	0.792	0.168	0.163	
Coef. var.	24.518	19.537	19.734	26.567	

42. Periploma subgracile (Whitfield) (Subequivalve)

N	7	7	7	7
Min.	8.300	5.900	1.200	5.500
Max.	34.500	26.900	4.700	20.300
Range	26.200	21.000	3.500	14.800
Mean	14.843	10.900	2.143	9.314
Std. dev.	9.398	7. 5 63	1.270	5.249
Var.	88.330	5 7. 203	1.613	2 7. 555
Coef. var.	63.319	69.388	59.266	56.357

43. Pholadomya deweyensis Speden (Equivalve)

N	6	6	6	6	5
Min.	4.300	3.100	1.100	1.200	17.000
Max.	29.20 0	21.700	6.800	7.100	20.000
Range	24.900	18.600	5.700	5.900	3.000
Mean	16.117	11.900	3.817	4.083	18.400
Std. dev.	9.381	7.062	2.131	2.142	1.140
Var.	8 7. 998	49.876	4.542	4.590	1.300
Coef. var.	58.205	59.347	5 5.83 7	52.466	6.197

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44. Goniomya americana Meek & Hayden (Equivalve)

	Length	Height	Half width	Anterior length	Length of nymph	Number of plicae
N	14	14	14	13	8	13
Min.	33.400	19.900	4.200	10.600	5.000	15.000
Max.	79.500	40.500	13.600	26.000	10.200	26.000
Range	46.100	20.600	9.400	15.400	5.200	11.000
Mean	51.679	26.714	7.729	15.508	6.700	19.769
Std. dev.	11.582	4.942	2.484	3.810	1.607	3,982
Var.	134.148	24. 426	6.168	14.512	2.583	15.859
Coef. var.	22.412	18.500	32.136	24.565	23.987	20.144

		45.	Cuspidaria	moreauensis	(Meek & Hay	<u>moreauensis</u> (Meek & Hayden) (Inequivalve)	ılve)		
	Length left	th right	Height left	ht right	Half width left	dth right	Width (both valves)	Anterior length left righ	length right
z	13	24	13	24	12	23	4	13	24
Min.	5,600	5.200	3,500	2.900	1.200	006.0	2,400	2,100	1,800
Max.	7.800	8,400	4, 900	5.500	1.900	2,100	3,800	3.200	3,600
Range	2,200	3,200	1.400	2,600	0.700	1.200	1.400	1.100	1.800
Mean	6,869	6.792	4.185	4.058	1.600	1,491	3,150	2.754	2.608
Std. dev.	0.816	006.0	0.476	0.579	0.226	0.307	0.597	0.393	0,391
Var.	999.0	608.0	0.226	0.336	0.051	0.094	0.357	0.154	0.153
Coef. var.	11,877	13,247	11.371	14.274	14.102	20,610	18,959	14.267	14,995

		46.	-	Cuspidaria ventricosa	(Meek & Hayo	(Meek & Hayden) (Inequivalve)	live)		
	left	Length right	Height left	ght right	Half width left	/dth right	Width (both valves)	Anterio left	Anterior length eft right
Z	ω	11	ω	11	9	10	64	ω	11
Min.	4.700	4,600	3,100	3,200	1.300	1.200	4.000	1.500	1.400
Max.	12,000	12,300	8.600	8,700	3,300	3.500	5.400	3,700	3.800
Range	7.300	7.700	5,500	5,500	2,000	2,300	1.400	2,200	2,400
Mean	8, 238	9,236	5, 562	6.218	2,300	2,480	4.700	2,538	2,773
Std. dev.	2,707	2,349	1,978	1,614	098.0	0.844	066 *0	0.798	0,683
Var.	7,326	5,517	3,911	2.604	0,740	0.713	0.980	0.637	0.466
Coef, var,	32,857	25,429	35, 554	25.949	37, 401	34,045	21,063	31,452	24,625

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PLATES

Abbreviations used in captions:

ANSP	Academy of Natural Sciences, Philadelphia
CIT	California Institute of Technology, Pasadena

GSC Geological Survey of Canada, Ottawa

UA University of Alberta, Edmonton
UCLA University of California, Los Angeles

USNM United States National Museum, Washington, D.C.

A YPM Invertebrate Paleontology collection numbers

AZ assemblage zone

Fig(s). Figure(s)
Loc. Locality

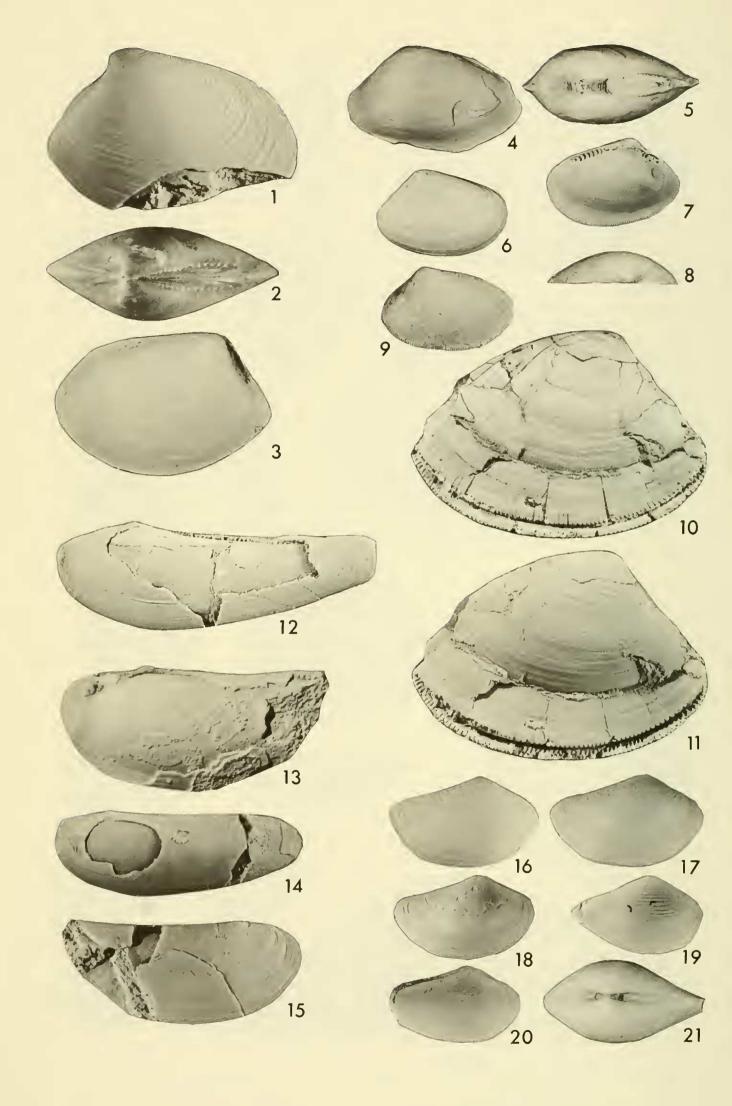
TCM Trail City Member
TLM Timber Lake Member
ILM Iron Lightning Member

LEl Little Eagle lithofacies, Trail City Member ICl Irish Creek lithofacies, Trail City Member

YPM Peabody Museum of Natural History, Yale University, New Haven, type

specimen numbers

All Yale Peabody Museum specimens illustrated were collected for this study except where noted otherwise. All figured specimens are shells unless otherwise indicated. All magnifications are given in linear factors.



Figs. 1-3. Nucula planomarginata Meek & Hayden

- 1. YPM 23954, A448, Loc. 56, ICl, TCM, Cymbophora-Tellinimera AZ. ×4.
- 2. YPM 23954, A448, Loc. 56, ICl, TCM, Cymbophora-Tellinimera AZ; dental socket pit visible. ×4.
- 3. YPM 23958, A746, Loc. 226, TLM, Cucullaea AZ; showing a smooth ventral margin. ×2.

Figs. 4-11. Nucula percrassa Conrad

- 4-5. YPM 23960, A428, Loc. 53, abyssinus concretion, LEI, TCM. ×1.
- 6. YPM 23959, A526, Meade County, Fox Hills Formation. ×1.
- 7. Ditto; hinge incomplete under umbone. $\times 1$.
- 8. Ditto. $\times 1$.
- 9. YPM 23962, A293, Loc. 25, LEI, TCM, above Protocardia-Oxytoma AZ; a steinkern. ×2.
- 10. YPM 23961, A278, Loc. 25, LEl, TCM, above *Protocardia-Oxytoma* AZ; uncoated, to show the dark lines under the fine costae. ×1.
- 11. Ditto; coated, to show the fine costae. $\times 1$.

Figs. 12-15. Nuculana (Nuculana) grandensis Speden, sp. n.

- 12. YPM 23985, A289, Loc. 25, LEI, TCM, above Protocardia-Oxytoma AZ; holotype. ×2.
- 13. YPM 23982, A457, Loc. 210, ICl, TCM, Cymbophora-Tellinimera AZ; specimen etched to show cast of resilifer pit under the umbone. ×6.
- 14. YPM 23984, A457, Loc. 210, ICl, TCM, Cymbophora-Tellinimera AZ; a juvenile specimen. ×4.
- 15. YPM 23983, A973, Loc. 100, ICl, TCM, Cucullaea AZ. ×4.

Figs. 16-21. Nuculana (Jupiteria) scitula (Meek & Hayden)

- 16. YPM 23968, A776, Loc. 227, abyssinus concretion, TLM. ×4.
- 17. YPM 23970, A779, Loc. 92, ICl, TCM, Cucullaea AZ. ×4.
- 18. YPM 23965, A799, Loc. 92, ICl, TCM, Cucullaea AZ. ×4.
- 19. YPM 24475, A799, Loc. 92, ICl, TCM, Cucullaea AZ. ×4.
- 20. YPM 23967, A677, Loc. 199, TCM, Limopsis-Pseudoptera AZ. ×4.
- 21. YPM 23966, A677, Loc. 199, TCM, Limopsis-Pseudoptera AZ; showing anterior and posterior external ligament. ×4.

Figs. 1-6. Nuculana (Jupiteria) scitula (Meek & Hayden)

- 1-2. YPM 23969, A458, Loc. 210, ICl, TCM, Cucullaea AZ. ×6.
- 3. YPM 24474, A477, Loc. 212, ICl, TCM, Cymbophora-Tellinimera AZ; a steinkern showing adductor and pedal muscle insertion areas. ×6.
- 4. YPM 23963, A458, Loc. 210, ICl, TCM, Cucullaea AZ; fragment of hinge showing small internal ligament pit. ×8.
- 5-6. YPM 23964, A504, Loc. 60, TLM, Cymbophora-Tellinimera AZ; left and right valve interiors showing hinges, pallial line and sinus, and adductor insertion areas. ×6.

Figs. 7-10. Yoldia lacrima Speden, sp. n.

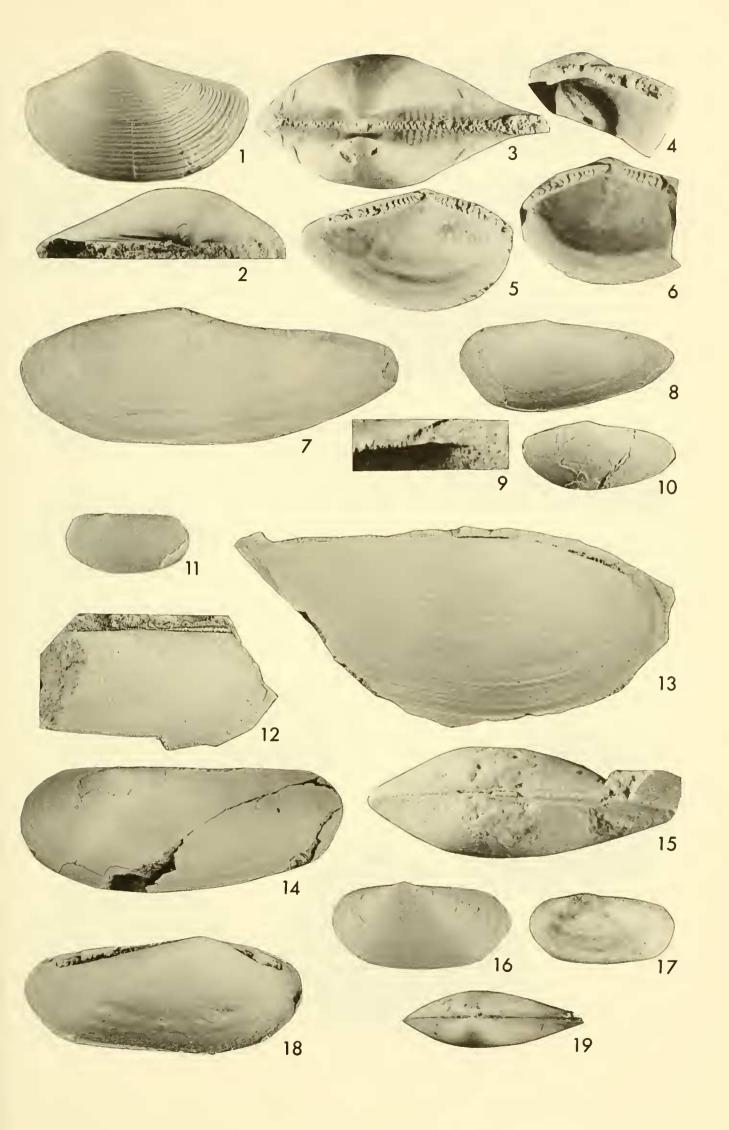
- 7. YPM 23987, A441, Loc. 56, ICl, TCM, Cymbophora-Tellinimera AZ; the largest specimen collected. ×2.
- 8. YPM 23988, A1032, Loc. 236, LEI, TCM, Lower nicolleti AZ; holotype. ×2.
- 9. YPM 24473, A531, Loc. 218, LEI, TCM, Lower nicolleti AZ; rubber latex cast of the center of the hinge showing the internal ligament pit. ×8.
- 10. YPM 23986, A1021, Loc. 235, LEI, TCM, Lower nicolleti AZ. ×4.

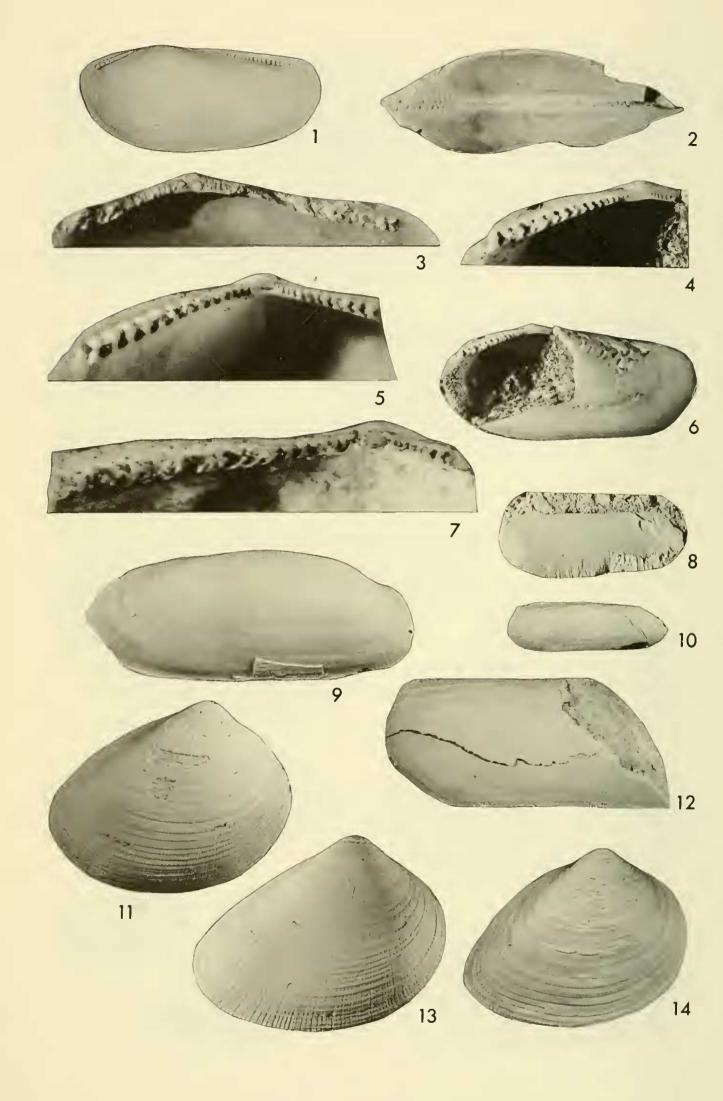
Figs. 11-14. Yoldia rectangularis Speden, sp. n.

- 11. YPM 23989, A1161, Loc. 118, LEI, TCM, Lower nicolleti AZ; a juvenile specimen. ×2.
- 12. YPM 23990, A1073, Loc. 243, LEI, TCM, Lower nicolleti AZ: a steinkern showing the small teeth and part of the pallial sinus . ×2.
- 13. YPM 23991, A659, Loc. 73, ICl, TCM, Cucullaea AZ; showing fine teeth, posterior adductor insertion area and, faintly, the anterior adductor insertion area and pallial sinus. ×2.
- 14. YPM 23992, A771, Loc. 88, TLM, abyssinus concretion; holotype. ×2.

Figs. 15-19. Malletia evansi (Meek & Hayden)

- 15. YPM 23976, A797, Loc. 92, ICl, TCM, Cucullaea AZ; showing most of the posterior external ligament. ×4.
- 16. YPM 23975, A1033, Loc. 236, LEI, TCM, Protocardia-Oxytoma AZ. ×4.
- 17. YPM 23977, A1244, Loc. 150, LEI, TCM, Protocardia-Oxytoma AZ; showing dental socket markings. ×4.
- 18. YPM 23972, A1334, Loc. 252, LEI, TCM, Protocardia-Oxytoma AZ; a large specimen with a postcrior taper. ×2.
- 19. YPM 23974, A791, Loc. 90, TLM, Sphenodiscus layer; showing the dorsal margin with the anterior and part of the posterior external ligament. ×4.





Figs. 1-7. Malletia evansi (Meek & Hayden)

- 1. YPM 23971, A285, Loc. 25, LEI, Protocardia-Oxytoma AZ; a steinkern. ×2.
- 2. YPM 23973, A477, Loc. 212, ICl, TCM, Cymbophora-Tellinimera AZ; interior of dorsal part of a shell showing incomplete posterior adductor insertion area and linear posterior pedal impressions. ×4.
- 3. YPM 23978, A973, Loc. 100, ICl, TCM, Cucullaea AZ; right valve hinge. ×8.
- 4. YPM 23981, A792, Loc. 90, TLM, Sphenodiscus layer; a right valve hinge. ×8.
- 5. YPM 23980, A793, Loc. 90, TLM, Cucullaea AZ; a right valve hinge. ×16.
- 6. YPM 23981, A792, Loc. 90, TLM, Sphenodiscus layer; a right valve. ×4.
- 7. YPM 23979, A799, Loc. 92, ICI, TCM, Cucullaea AZ; a left valve hinge. ×16.

Figs. 8-10, 12. Solemya subplicata (Meek & Hayden)

- 8. YPM 23996, A635, Loc. 69, LEI, TCM, Protocardia-Oxytoma AZ; posterior end crushed. ×4.
- 9. YPM 23995, A791, Loc. 90, TLM, Sphenodiscus layer; a steinkern showing posterior adductor insertion area. ×2.
- 10. YPM 23993, A1043, Loc. 238, LEI, TCM, Limopsis-Pseudoptera AZ; posterior end crushed. ×1.
- 12. YPM 23994, A623, Loc. 222, LEI, TCM, Lower nicolleti AZ. ×2.

Figs. 11, 13, 14. Limopsis striatopunctatus Evans & Shumard

- 11. YPM 23998, A1043, Loc. 238, LEI, TCM, Limopsis-Pseudoptera AZ. ×2.
- 13. YPM 24001, A1043, Loc. 238, LEI, TCM, Limopsis-Pseudoptera AZ. ×2.
- 14. YPM 23997, A1043, Loc. 238, LEI, TCM, Limopsis-Pseudoptera AZ. ×2.

(See Plate 5 for other specimens of Limopsis striatopunctatus from the same concretion and showing marked variation in shape).

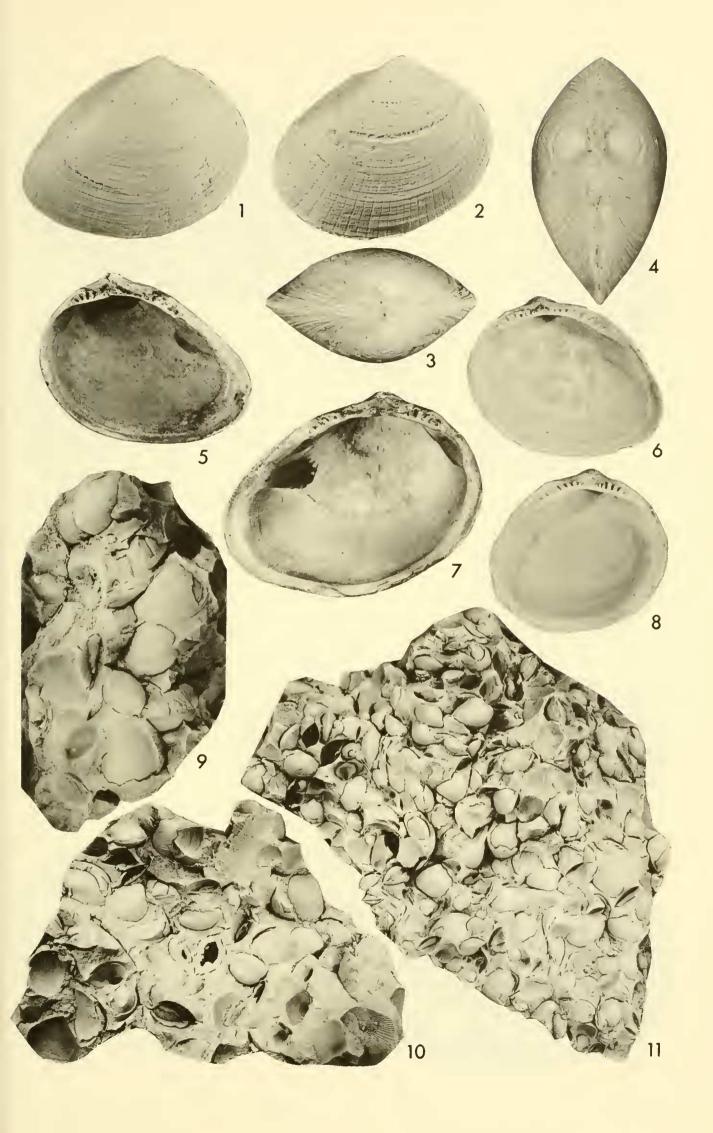
Figs. 1-11. Limopsis striatopunctatus Evans & Shumard

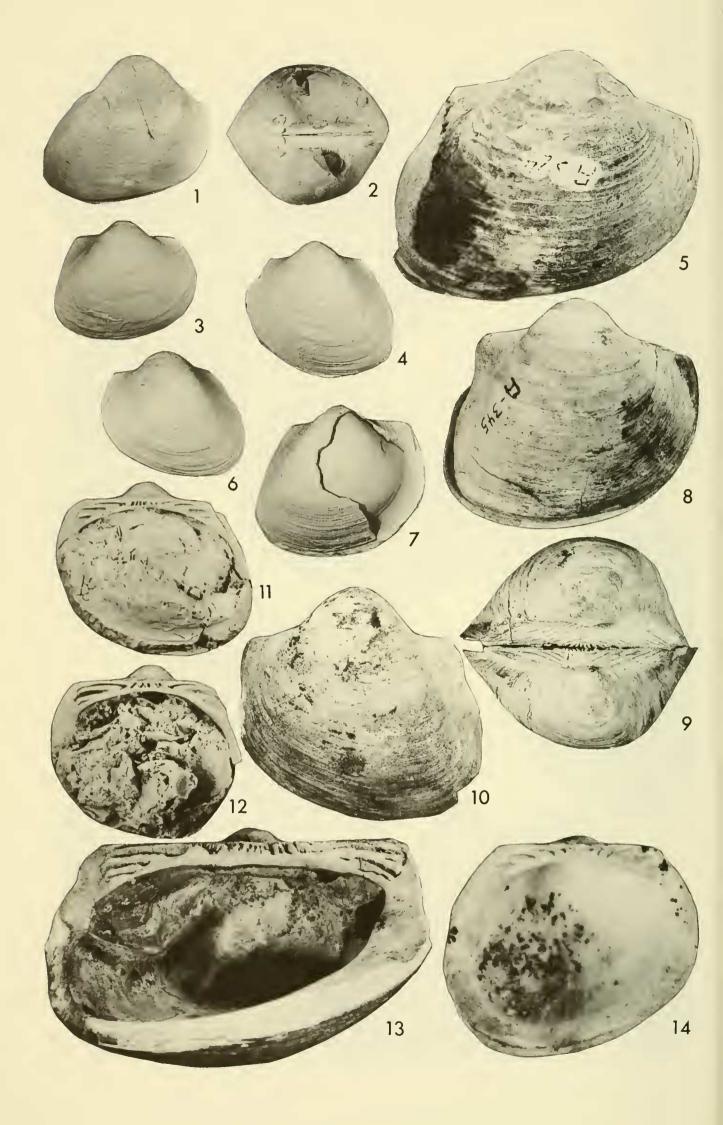
- 1. YPM 23999, A1043, Loc. 238, LEI, TCM, Limopsis-Pseudoptera AZ. ×2.
- 2-3. YPM 24000, A1043, Loc. 238, LEI, TCM, Limopsis-Pseudoptera AZ. ×2.
- 4. YPM 24001, A1043, Loc. 238, LEI, TCM, Limopsis-Pseudoptera AZ. ×2.
- 5. YPM 24002, A677, Loc. 199, LEI, TCM, Limopsis-Pseudoptera AZ. ×2.
- 6. YPM 24004, A677, Loc. 199, LEI, TCM, Limopsis-Pseudoptera AZ. ×4.
- 7. YPM 24005, A693, Loc. 204, LEI, TCM, Limopsis-Pseudoptera AZ; showing two buttresses in the ligament pit. ×2.
- 8. YPM 24003, A677, Loc. 199, LEI, TCM, Limopsis-Pseudoptera AZ. ×4.

(The interiors, figs. 5-8, show hinges, ligament areas, adductor and pedal muscle insertion areas, and fine radial costae).

- 9. YPM 24007, A565, Loc. 119, LEI, TCM, Limopsis-Pseudoptera AZ. ×1.
- 10. YPM 24006, A1109, Loc. 105, LEI, TCM, Limopsis-Pseudoptera AZ. ×1.
- 11. YPM 24008, A1020, Loc. 235, LEI, TCM, Limopsis-Pseudoptera AZ. ×1.

(The three blocks of concretions illustrated by figs. 9-11 show different ranges and a uniformity of size classes in each block).





Figs. 1-14. Cucullaea nebrascensis Owen

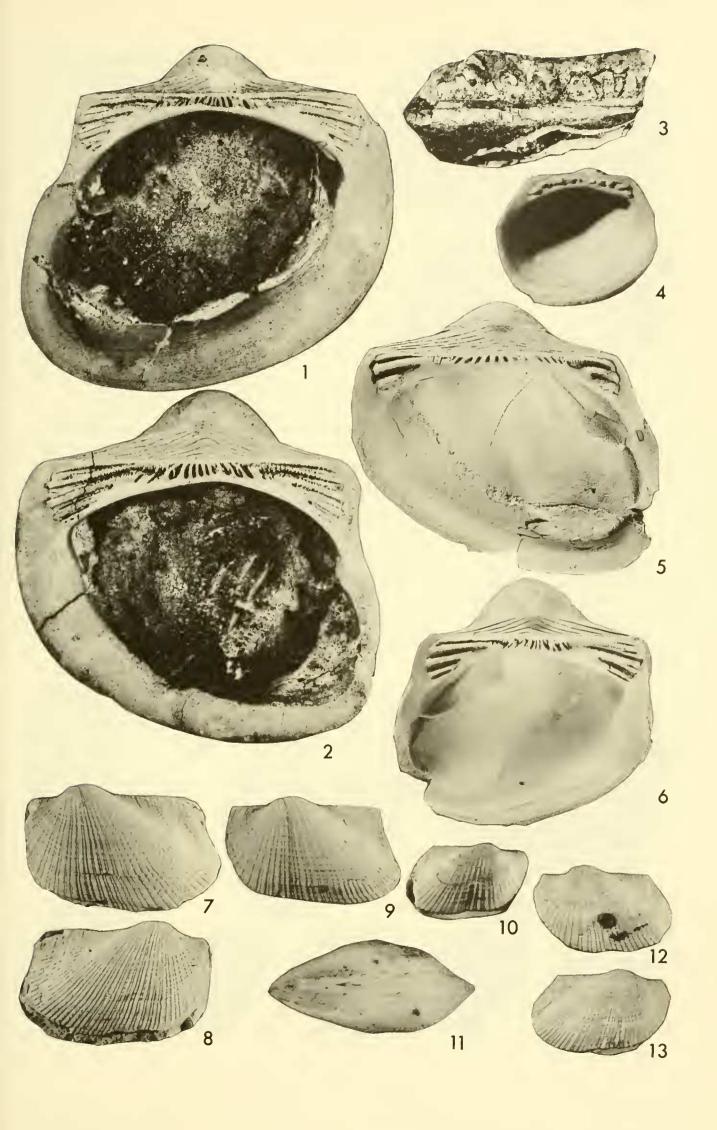
- 1. YPM 24663, A348, Loc. 37, TLM, Cucullaca AZ; showing the inequivalve ventral margin and the radial structure of the outer shell layer. $\times 0.5$.
- Ditto; showing remnants of the inner ligament layer along the commissure. $\times 0.5$. 2.
- YPM 24660, A347, Loc. 36, ICl, TCM, Cucullaea AZ. ×1. YPM 24659, A650, Loc. 73, ICl, TCM, Cucullaea AZ. ×1. 3.
- 4.
- YPM 24664, A324, Loc. 28, TLM, Cucullaea AZ; shows the radial structure in the outer 5. shell layer. $\times 1$.
- YPM 24661, A347, Loc. 36, ICl, TCM, Cucullaea AZ. ×1. 6.
- YPM 24662, A474, Loc. 212, ICl, TCM, Cucullaea AZ. ×1.
- 8-9. YPM 24666, A345, Loc. 35, TLM, Cucullaea AZ; notice the strongly inequivalve ventral margin on fig. 8. $\times 1$.
- 10. YPM 24665, A345, Loc. 35, TLM, Cucullaea AZ. ×1.
- 11. YPM 23903, A920, Loc. 92, ICl, TCM, Cucullaea AZ. ×1.5.
- YPM 23909, A460, Loc. 210, ICI, TCM, Cucullaea AZ. ×1.5. 12.
- YPM 24665, A345, Loc. 35, TLM, Cucullaea AZ; showing the buttress which carries the 13. posterior adductor insertion area, the lined region of the posterior pedal retractor, the pallial attachment band under the hinge margin, the anterior adductor and pedal impressions, and serrations on the teeth. $\times 1.5$.
- 14. YPM 23904, A973, Loc. 100, ICl, TCM, Cucullaea AZ. ×8.

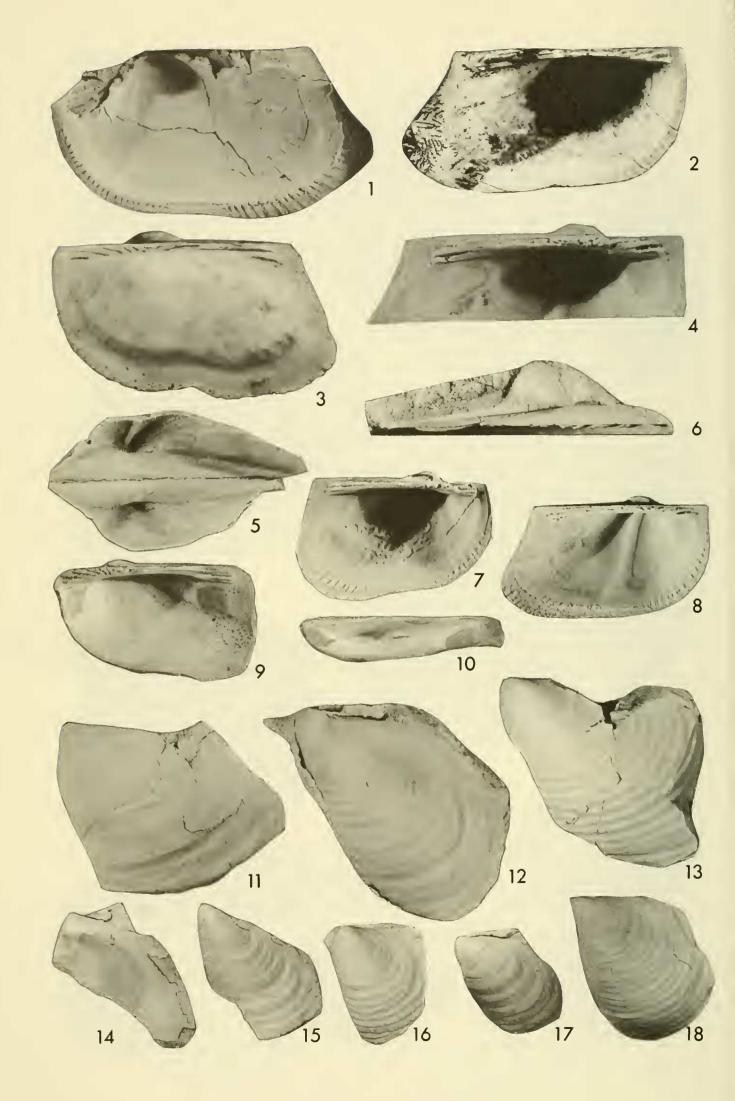
Figs. 1-6. Cucullaea nebrascensis Owen

- 1-2. YPM 24666, A345, Loc. 35, TLM, *Cucullaea* AZ; compare with figs. 8 and 9 of Pl. 6. ×1.5.
- 3. YPM 24105, A321, Loc. 28, TLM, Cucullaea AZ; part of hinge showing a rod of dark chitinous outer ligament along the commissure, and its branches to the chevrons (the thin bands in the fibrous inner ligament). ×2.
- 4. YPM 23882, A655, Loc. 73, ICl, TCM, Cucullaea AZ. ×8.
- 5. YPM 24664, A324, Loc. 28, TLM, Cucullaea AZ. ×1.
- 6. YPM 24665, A345, Loc. 35, TLM, Cucullaea AZ. ×1.

Figs. 7-13. Parallelodon (Cosmetodon) sulcatinus (Evans & Shumard)

- 7-8. YPM 24026, A933, Loc. 95, LEI, TCM, Limopsis-Pseudoptera AZ; note the more coarse costation of the left valve. ×4.
- 9. YPM 24027, A677, Loc. 199, LEI, TCM, Limopsis-Pseudoptera AZ. ×6.
- 10. YPM 24024, A561, Loc. 64, LEI, TCM, Limopsis-Pseudoptera AZ; showing the inequivalveness and no byssal gape on a small specimen. ×6.
- 11-13. YPM 24022, A1006, Loc. 233, LEI, TCM, Limopsis-Pseudoptera AZ; note the more numerous costae on the left valve, and the morphology of the cardinal area. Fig. 11 × 9, figs. 12 and 13 × 4.





Figs. 1-10. Parallelodon (Cosmetodon) sulcatinus (Evans & Shumard)

- YPM 24025, A1114, Loc. 106, LEl, TCM, Limopsis-Pseudoptera AZ; internal view of 1. an incomplete right valve, showing marginal crenulate projections and the impression of the inequivalve overlap of the left valve. $\times 4$.
- YPM, 24023, A933, Loc. 95, LEI, TCM, Limopsis-Pseudoptera AZ; showing marked 2. posteroventral attenuation. ×4.
- YPM 23916, A677, Loc. 199, LEI, TCM, Limopsis-Pseudoptera AZ; showing a smooth 3. band across the weak sulcus of the right valve. $\times 6$.
- YPM 23941, A1061, Loc. 242, LEI, TCM, Limopsis-Pseudoptera AZ; a dorsal view of 4. the ligament area showing three opisthodetic ligament grooves. $\times 4$.
- YPM 24020, A1104, Loc. 249, LEI, TCM, Limopsis-Pseudoptera AZ; showing internal 5. umbonal characteristics and the pallial attachment band along the commissure. $\times 4$.
- YPM 23941, A1061, Loc. 242, LEI, TCM, Limopsis-Pseudoptera AZ; showing hinge and 6.
- internal morphology. Note the strong rib on the interior surface of the sulcus. ×4. YPM 23934, A1021, Loc. 235, LEI, TCM, Limopsis-Pseudoptera AZ; showing the strong 7. crenulations situated above the ventral margin and for the interlocking of the right valve, and the smooth zone across the sulcus. $\times 4$.
- YPM 23941, A1061, Loc. 242, LEI, TCM, Limopsis-Pseudoptera AZ; showing hinge and 8. internal morphology. ×4.
- 9-10. YPM 23912, A677, Loc. 199, LEI, TCM, Limopsis-Pseudoptera AZ; showing hinge and muscle insertion areas, pedal impressions, and the prominent linear scar on the posterior flank of the umbonal cavity. $\times 4$.

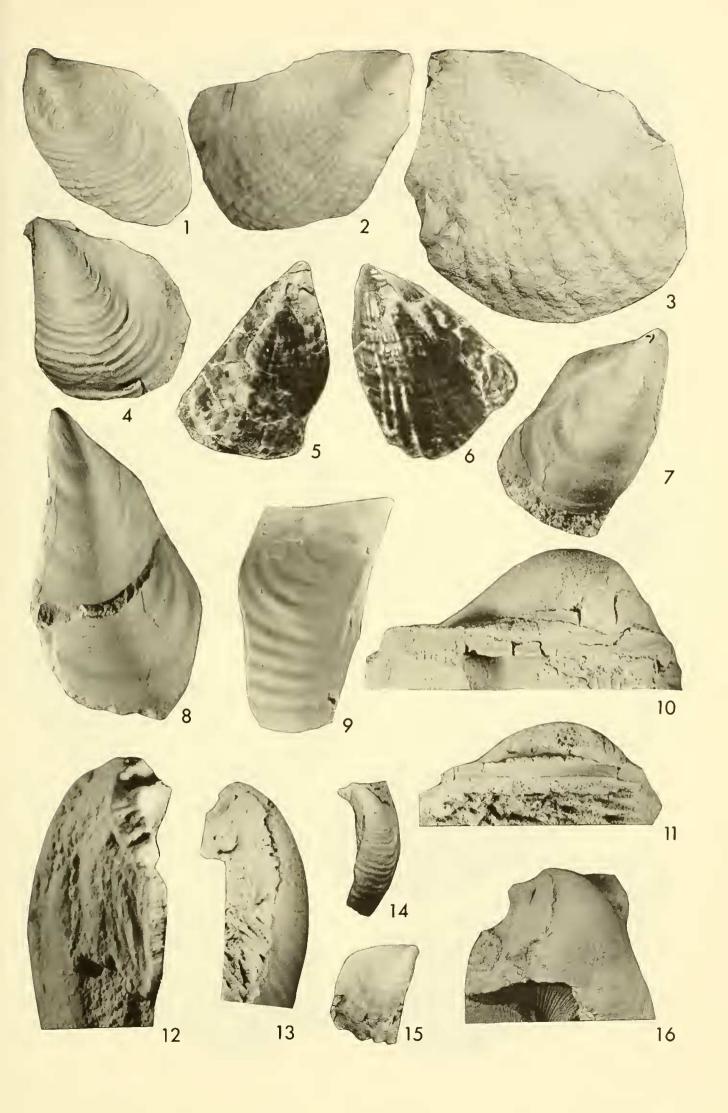
Figs. 11-18. Tenuipteria fibrosa (Meek & Hayden)

- 11. YPM 24742, A525, Loc. 9, LEI, TCM, Upper nicolleti AZ. ×1.
- 12. YPM 24029, A990, Loc. 231, LEI, TCM, Lower nicolleti AZ; showing narrow projecting anterior ear and the dorsal border of the prismatic shell layer (see also figs. 14 and 17). $\times 2$.
- 13. YPM 24035, A635, Loc. 69, LEI, TCM, Upper nicolleti AZ. ×1.
- 14. YPM 24030, A990, Loc. 231, LEI, TCM, Upper nicolleti AZ; showing the outline of the inner shell layer situated well inside the incomplete posterodorsal margin of the outer prismatic shell layer. $\times 1$.
- 15. YPM 24648, A270, Loc. 21, LEI, TCM, Lower nicolleti AZ. ×1.
 16. YPM 24036, A723, Loc. 82, LEI, TCM, Upper nicolleti AZ. ×1.
- 17. YPM 24643, A1084, Loc. 246, LEI, TCM, Lower nicolleti AZ. Note the two orders of concentric plicae. ×1.
- 18. YPM 24647, A410, Loc. 51, LEl, TCM, Upper nicolleti AZ. ×1.

(Specimens showing the weak radial ornament and stronger concentric plicae characteristic of Fox Hills Formation samples).

Figs. 1-16. Tenuipteria fibrosa (Meek & Hayden)

- 1. YPM 24646, A336, Loc. 32, Mobridge Member, Pierre Shale. ×1.
- 2-3. YPM 24039, A336, Loc. 32, Mobridge Member, Pierre Shale; note the wide ventral flange of outer shell layer. ×1.
- 4. YPM 24033, A992, Loc. 231, LEI, TCM, Lower nicolleti AZ; showing the divergence of the outer prismatic shell layer from the inner layer dorsally. ×1.
- 5-6. YPM 24028, A336, Loc. 32, Mobridge Member, Pierre Shale; showing faint outline of the large oval posterior adductor insertion area at the posteroventral extremity of the inner shell layer. ×2.
- 7. YPM 24037, A350, Loc. 39, TLM, Cucullaea AZ; showing posteroventrally situated posterior adductor insertion area and the two anterior byssal insertion areas on either side of the fracture on the umbone. ×6.
- 8. YPM 24038, A350, Loc. 39, TLM, Cucullaea AZ; showing the anterodorsal byssal impression and a pallial line that is continuous almost to the scar. ×4.
- 9. YPM 24034, A959, Loc. 104, LEI, TCM, Lower nicolleti AZ; showing the two dorsal byssal impressions, a discontinuous pallial line, and cross-plaits on a reflexed anterodorsal area. ×4.
- 10. YPM 24644, A1140, Loc. 115, LEI, TCM, Protocardia-Oxytoma AZ; showing ligament area and form of the anterior ear. ×3.
- 11. YPM 24033, A992, Loc. 231, LEI, TCM, Lower *nicolleti* AZ; showing the striated ligament area which lacks ligament pits. ×4.
- 12. YPM 24032, A990, Loc. 231, LEI, TCM Lower nicolleti AZ; showing the wide flange of outer prismatic shell layer forming the anterior ear and the concave form of the ligament area. ×8.
- 13. YPM 24033, A992, Loc. 231, LEI, TCM, Lower nicolleti AZ; showing the reflected base of the anterior ear. ×2.
- 14. YPM 24031, A990, Loc. 231, LEI, TCM, Lower nicolleti AZ; showing the anterior ear and the inturned anterodorsal margin. ×1.
- 15. YPM 24645, A313, Loc. 27, LEI TCM, abyssinus concretion; a strongly radially sulcate specimen. ×1.
- 16. YPM 24644, A1140, Loc. 115, LEI, TCM, Protocardia-Oxytoma AZ; showing ligament area and form of the anterior ear. ×1.5.



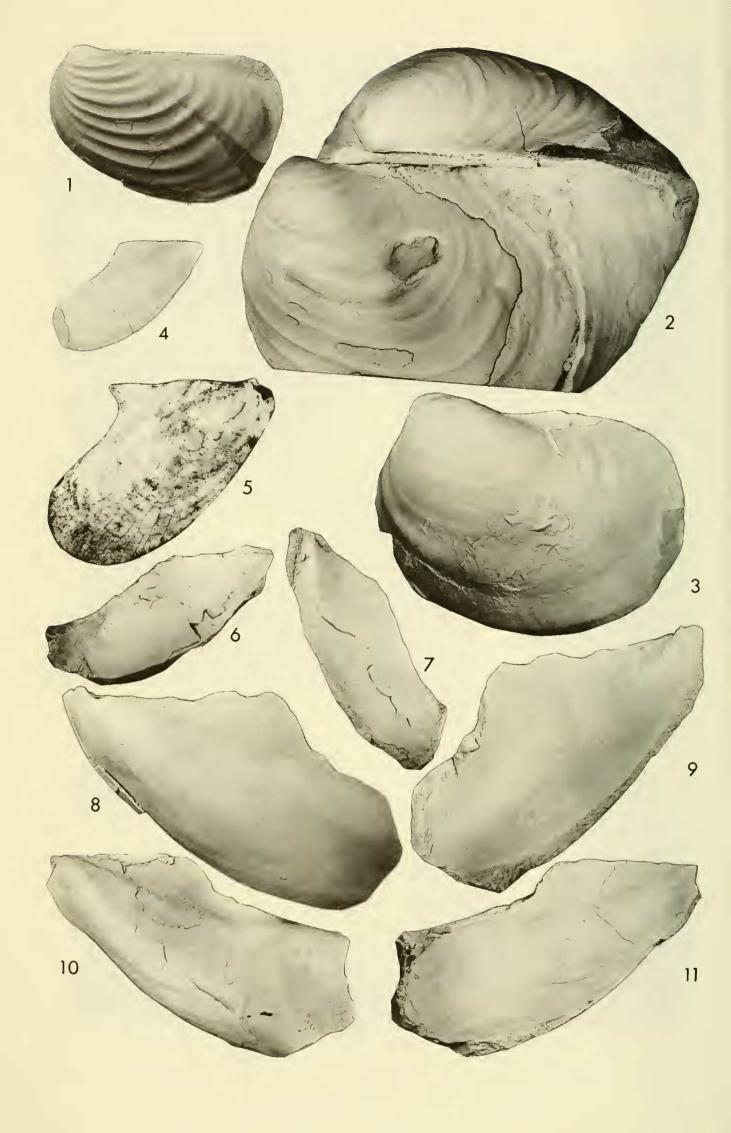


Fig. 1. "Endocostea" typica White

1. YPM 24053, Converse County, Wyoming, Pierre Shale; showing the anterodorsal byssal-pedal muscle insertions and, very faintly across the base of the "endocosta", the posteroventral adductor insertion. ×1.

Figs. 2, 3. "Inoceramus" of the barabini Morton complex

- 2. YPM 24055; showing small ligament pits on the dorsal half of the ligament area. ×1.
- 3. YPM 24052; showing the anterodorsal byssal-pedal insertions, posterodorsal adductor insertion, the pallial line of discontinuous insertions, and mantle attachment insertions across the dorsal part of the steinkern. ×1.

Both collected by C. E. Beecher and J. B. Hatcher, Converse County, Wyoming, Pierre Shale.

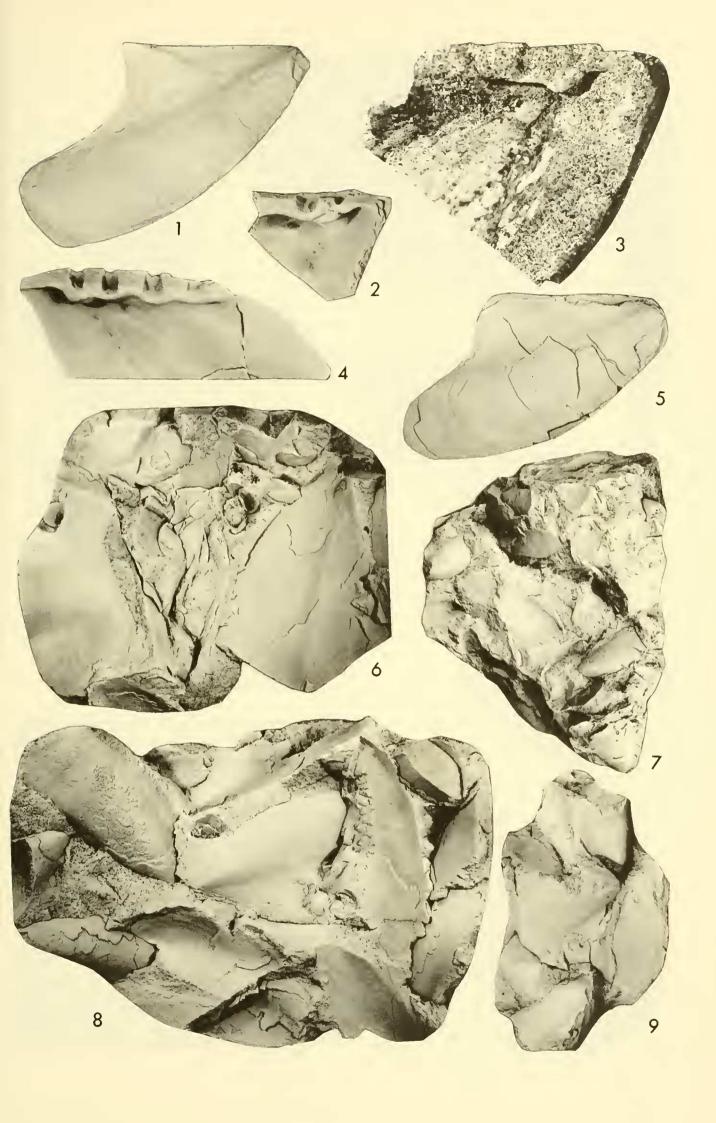
Figs. 4-11. Pseudoptera subtortuosa (Meek & Hayden)

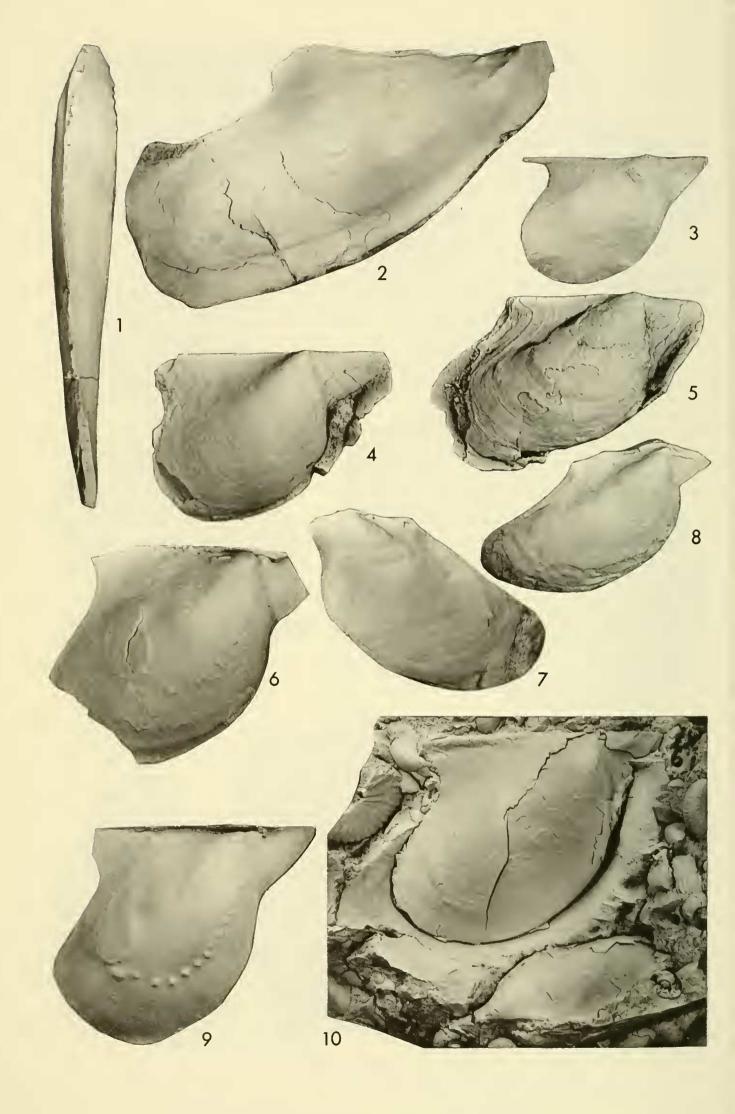
- 4. YPM 24050, A1123, Loc. 239, LEI, TCM, Limopsis-Pseudoptera AZ. ×1.
- 5. YPM 24049, A1058, Loc. 241, LEI, TCM, Limopsis-Pseudoptera AZ; a juvenile with a prominent posterior ear. ×2.
- 6-7. YPM 24042, A1128, Loc. 108, LEI, TCM, *Protocardia-Oxytoma* AZ; a long narrow specimen. ×0.5.
- 8-9. YPM 24045, A273, Loc. 21, LEI, TCM, Limopsis-Pseudoptera AZ; showing muscle insertion areas and the larger left valve. ×1.
- 10-11. YPM 24046, A659, Loc. 73, ICl, TCM, Cucullaea AZ; note the greater inflation of the left valve (fig. 10) and the radial costae on fig. 11. ×1.

Figs. 1-9. Pseudoptera subtortuosa (Meek & Hayden)

- 1. YPM 24040, A1307, Loc. 177, LEI, TCM, Limopsis-Pseudoptera AZ. ×1.
- 2. YPM 24043B, A356, Loc. 44, LEI, TCM, Limopsis-Pseudoptera AZ; ventral view of the anterior part of the hinge and ligament area, and muscle insertions in the umbone. ×2.
- 3. YPM 24048, A724, Loc. 83 TLM Tancredia-Ophiomorpha Biofacies; showing dark band of outer shell layer around the anterior ear. ×1.
- 4. YPM 24051, A1336, Loc. 252, LEI, TCM, Limopsis-Pseudoptera AZ; showing ligament area and hinge. ×2.
- 5. YPM 24043A, A356, Loc. 44, LEI, TCM, Limopsis-Pseudoptera AZ; a specimen with a low height to length ratio. Compare with figure 1. ×1.
- 6. YPM 24043, A356, Loc. 44, LEI, TCM, Limopsis-Pseudoptera AZ; a block with specimens of two size classes. ×1.
- 7. YPM 24041, A1150, Loc. 115, LEI, TCM, Limopsis-Pseudoptera AZ. ×1.
- 8. YPM 24487, A1172, Loc. 110, LEI, TCM, Limopsis-Pseudoptero AZ. ×1.
- 9. YPM 24744, A1150, Loc. 115, LEI, TCM, Limopsis-Pseudoptera AZ; see figure 7 for a block from the same concretion but having a different size class. ×1.

(Figs. 6-9 show different size classes found in separate or the same assemblages).





Figs. 1-2. Pseudoptera subtortuosa (Meek & Hayden)

1-2. YPM 24047, A243, Loc. 11, LEI, TCM, Lower nicolleti AZ; a steinkern showing muscle insertion areas, discontinuous pallial line, and ventral twisting of the valves. ×1.

Figs. 3-10. Phelopteria linguaeformis (Evans & Shumard)

- 3. YPM 24058, A345, Loc. 35, TLM, Cucullaea AZ. ×2.
- 4. YPM 24074, A318, Loc. 28, TLM, Cucullaea AZ. ×1.
- 5. YPM 24071, A724, Loc. 83, TLM, Tancredia-Ophiomorpha Biofacies; showing ornament on the outer surface of the outer shell layer, and the relationship of the anterior ears of the valves (see also fig. 4 and Pl. 13, fig. 1). ×1.
- 6. YPM 24062, A1262, Loc. 161, ICl, TCM; showing posterior adductor insertion and pallial line of discrete scars (see also fig. 9). ×2.
- 7-8. YPM 24064, A324, Loc. 28, TLM, Cucullaea AZ; steinkerns of matching right and left valves, markedly different in shape, especially the right valve which has a wide flange of outer shell layer greatly extended posteroventrally. ×1.
- 9. YPM 24061, A1262, Loc. 161, 1Cl, TCM; see also figure 6. ×2.
- 10. YPM 24607A, A659, Loc. 73, ICl, TCM, Cucullaea AZ; on a block (YPM 24067) with large and very small specimens. ×1.

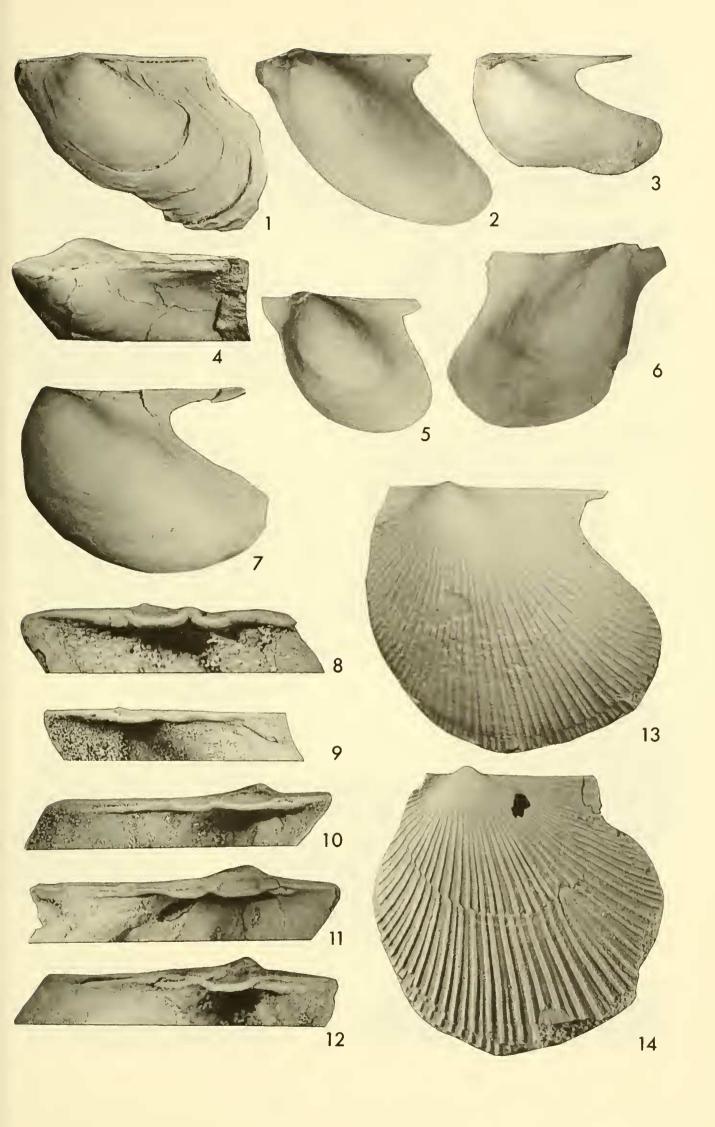
Figs. 1-12. Phelopteria linguaeformis (Evans & Shumard)

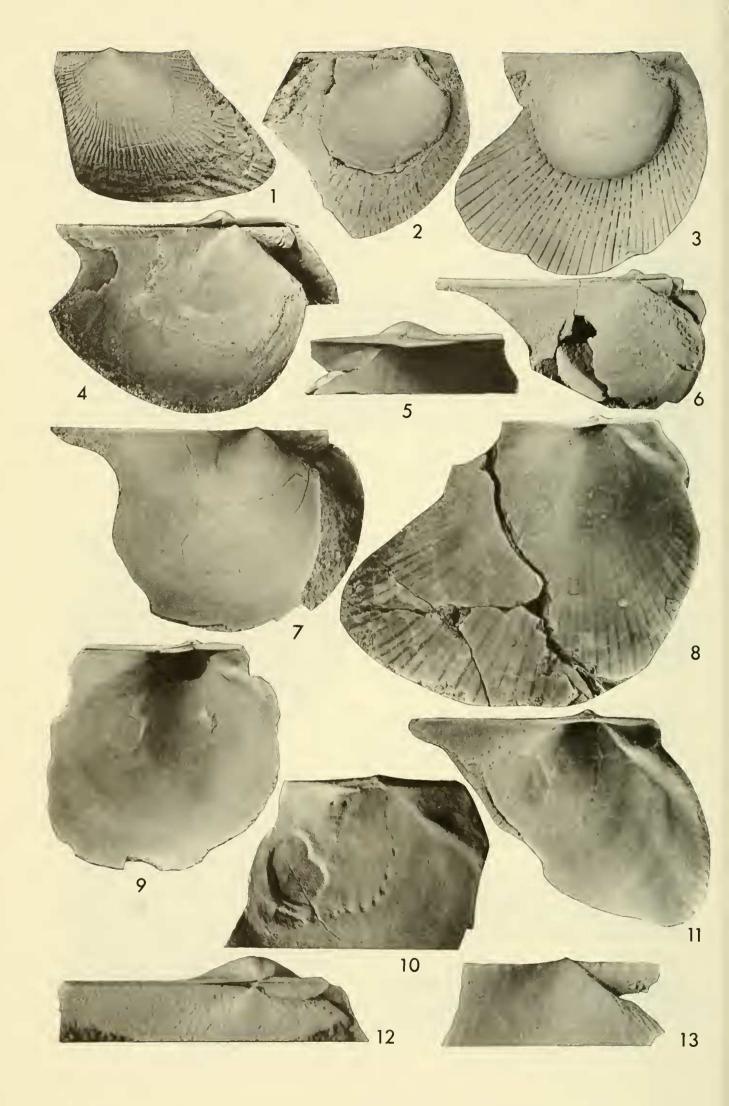
- 1. YPM 24071, A724, Loc. 83, TLM, Tancredia-Ophiomorpha Biofacies; a left valve with outer shell layer showing ornament. ×2.
- 2. YPM 24065, A324, Loc. 28, TLM, Cucullaea AZ; a specimen with a large angle, and squarish adductor muscle insertion area. ×2.
- 3. YPM 24059, A329, Loc. 30, TLM, Cucullaea AZ; showing typical pointed posterior ear, and the broken margin of outer shell layer. ×1.
- 4. YPM 24066, A1026, Loc. 139, ICl, TCM, Cymbophora-Tellinimera AZ; showing ligament area. ×1.5.
- 5. YPM 24057, A760, Loc. 88, TLM, Cucullaea AZ. ×1.5.
- 6. YPM 24056, A316, Loc. 28, TLM, Cucullaea, AZ. ×1.5.
- 7. YPM 24060, A348, Loc. 37, TLM, Cucullaea AZ. ×1.5.
- 8. YPM 24073, A724, Loc. 83, TLM, Tancredia-Ophiomorpha Biofacies. ×3.
- 9. YPM 24072, A724, Loc. 83, TLM, Tancredia-Ophiomorpha Biofacies. ×2.
- 10. YPM 24068, A724, Loc. 83, TLM, Tancredia-Ophiomorpha Biofacies. ×2.
- 11. YPM 24069, A724, Loc. 83, TLM, Tancredia-Ophiomorpha Biofacies. ×2.
- 12. YPM 24070, A724, Loc. 83, TLM, Tancredia-Ophiomorpha Biofacies. ×3.

Figs. 8-10 show ligament areas and hinges.)

Figs. 13, 14. Oxytoma (Hypoxytoma) nebrascana (Evans & Shumard)

- 13. YPM 24090, A379, Loc. 50, LEI, TCM, Protocardia-Oxytoma AZ. ×2.
- 14. YPM 24078, A1039, Loc. 237, LEI, TCM, Protocardia-Oxytoma AZ; showing smooth umbone and costation. ×4.



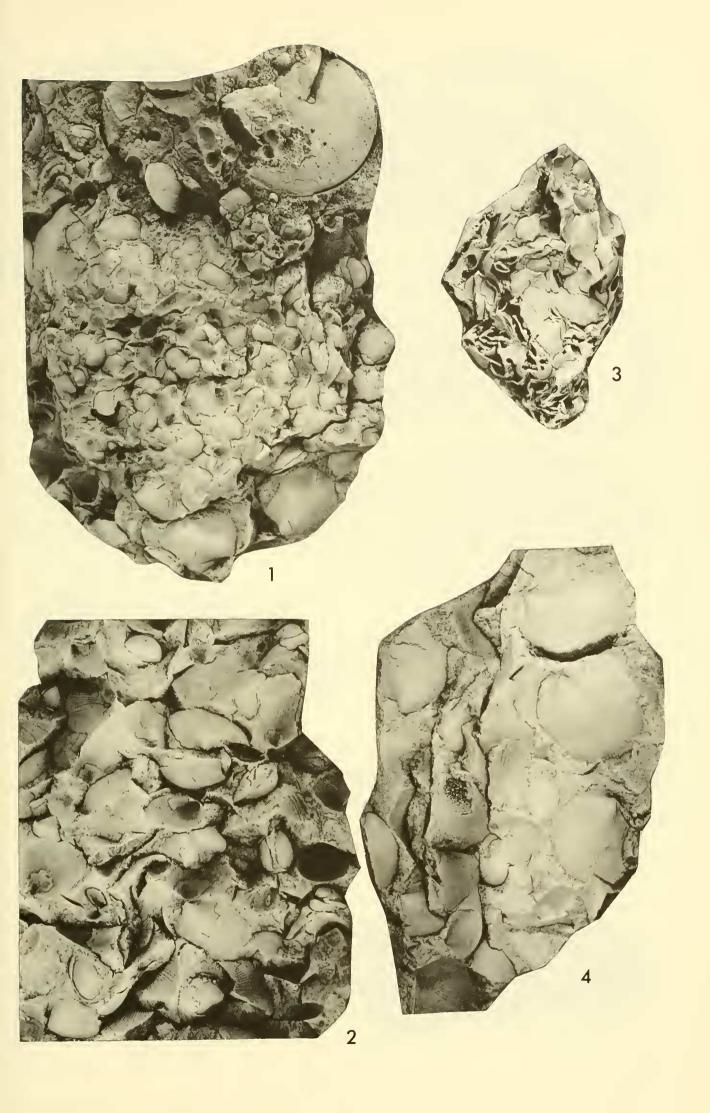


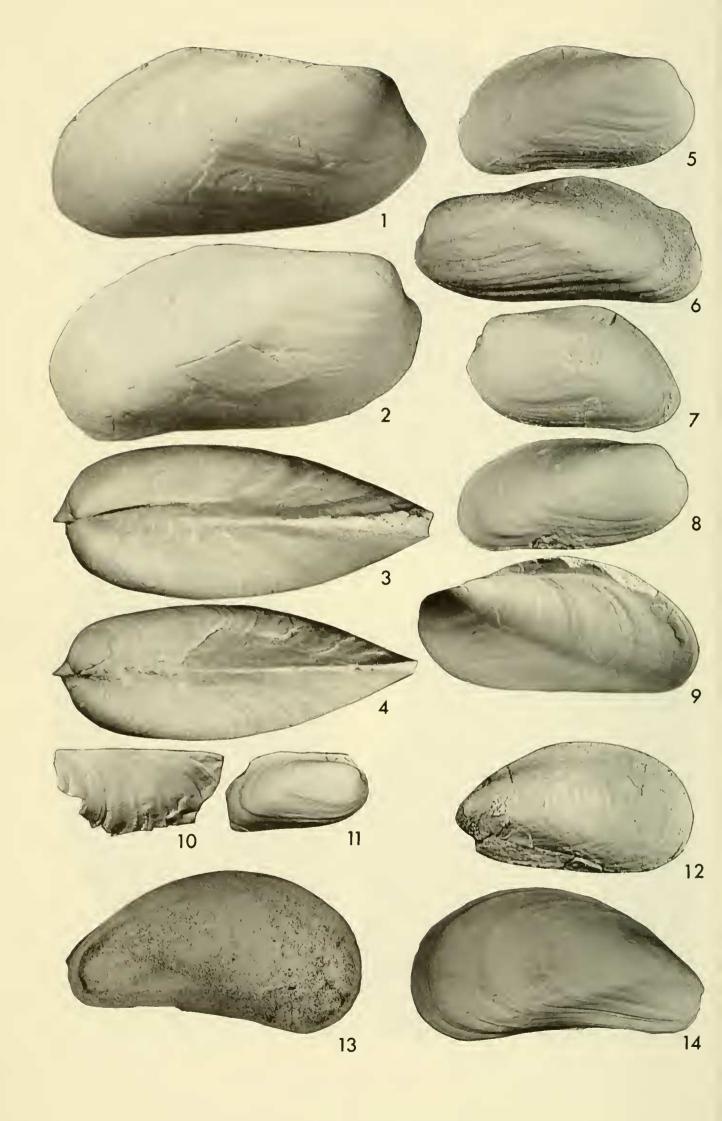
Figs. 1-13. Oxytoma (Hypoxytoma) nebrascana (Evans & Shumard)

- 1. YPM 24083, A1170, Loc. 110, LEI, TCM, Limopsis-Pseudoptera AZ; a very subquadrate specimen. ×2.
- 2. YPM 24080, A581, Loc. 191, LEI, TCM, Protocardia-Oxytoma AZ; showing the reflexion of the right valve. ×2.
- 3. YPM 24076, A297, Loc. 25, LEI, TCM, Protocardia-Oxytoma AZ; showing marked inequivalveness of the inflated part of the right valve (see also fig. 2). ×2.
- 4. YPM 24088, A1342, Loc. 253, LEl, TCM, Protocardia-Oxytoma AZ; showing the fine reticulated ornament of the right valve. ×2.
- 5. YPM 24085, A724, Loc. 83, TLM, Tancredia-Ophiomorpha Biofacies; showing interior and exterior of the byssal ear, ligament area, etc. ×4.
- 6. YPM 24079, A1039, Loc. 237, LEl, TCM, *Protocardia-Oxytoma* AZ; showing morphology of the posterior ear. $\times 4$.
- 7. YPM 24084, A1170, Loc. 110, LEI, TCM, Limopsis-Pseudoptera AZ; showing the fine reticulate ornament of the right valve. ×2.
- 8. YPM 24075, A279, Loc. 110, LEI, TCM, Protocardia-Oxytoma AZ; showing plication of the ventral half of the left valve, and muscle insertion areas. ×2.
- 9. YPM 24086, A724, Loc. 83, TLM, Tancredia-Ophiomorpha Biofacies; interior of a left valve, showing muscle insertion areas and ligament area. ×4.
- 10. YPM 24082, A1170, Loc. 110, LEI, TCM, Limopsis-Pseudoptera AZ; showing posterior adductor insertion, gill suspensory insertion, and pallial line of discrete small insertions. ×4.
- 11. YPM 24081, A1170, Loc. 110, LEI, TCM, Limopsis-Pseudoptera AZ; internal morphology, especially the wavy pattern on the inner shell surface due to the concentric cross-lamellar structure. ×2.
- 12. YPM 24078, A1039, Loc. 237, LEI, TCM, Protocardia-Oxytoma AZ. ×4.
- 13. YPM 24085, A724, Loc. 83, TLM, Tancredia-Ophiomorpha Biofacies; showing interior and exterior of the byssal ear, ligament area, etc. ×4.

Figs. 1-4. Oxytoma (Hypoxytoma) nebrascana (Evans & Shumard)

- 1-2. YPM 24087, A1141, Loc. 115, LEI, TCM, Limopsis-Pseudoptera AZ; front and back of the same block, showing a "cluster" of small specimens of Oxytoma surrounded by large specimens of Oxytoma and Limopsis, plus incomplete specimens of the ammonoids Sphenodiscus and Discocaphites. ×1.
- 3. YPM 24089, A585, Loc. 64, LEI, TCM, Limopsis-Pseudoptera AZ; part of a concretion composed almost wholly of small specimens of Oxytoma, many of which are hollow. ×1.
- 4. YPM 24090, A379, Loc. 50, LEI, TCM, Protocardia-Oxytoma AZ; compare the uniform large size of specimens in this block with the size ranges shown in figures 1-3. ×1.





Figs. 1, 3, 5-11. Modiolus meeki (Evans & Shumard)

- 1, 3. YPM 24108, A567, Loc. 191, LEI, TCM, Protocardia-Oxytoma AZ; compare to figs. 2, 4. ×4.
- 5. YPM 24107, A1008, Loc. 233, LEI, TCM, Protocardia-Oxytoma AZ. ×2.
- 6. YPM 24110, A282, Loc. 25, LEI, TCM, Limopsis-Pseudoptera AZ. ×1.
- 7. YPM 24109, A746, Loc. 226, TLM, Cucullaea AZ. ×2.
- 8. YPM 24106, A1008, Loc. 233, LEI, TCM, Protocardia-Oxytoma AZ. ×2.
- 9. YPM 24113, A1227, Loc. 145, LEI, TCM, Protocardia-Oxytoma AZ; showing the outline of the ventral part of the posterior adductor insertion. ×4.
- 10. YPM 24112, A724, Loc. 83, TLM, Tancredia-Ophiomorpha Biofacies; showing external ornament. ×2.
- 11. YPM 24111, A282, Loc. 25, LEI, TCM, Limopsis-Pseudoptera AZ. ×1.

Figs. 2, 4. Modiolus uddeni Stephenson

2, 4. USNM 76493, USGS Loc. 762, Navarro Group, Texas, Maestrichtian; showing regular plicae on umbones, and shape differences. ×4.

Figs. 12-14. Modiolus galpinianus (Evans & Shumard)

- 12. YPM 24120, A724, Loc. 83, Tancredia-Ophiomorpha Biofacies; showing shape and ornament. ×2.
- 13-14. YPM 24118, A724, Loc. 83, TLM, Tancredia-Ophiomorpha Biofacies; interior and exterior. ×1.5.

Figs. 1-3. Modiolus galpinianus (Evans & Shumard)

- 1. YPM 24698, A950, Loc. 97, Colgate lithofacies, ILM; showing adductor and posterior pedal insertions, and pallial line. ×1.5. 2. YPM 24119, A724, Loc. 83, TLM, Tancredia-Ophiomorpha Biofacies; an incomplete
- specimen, showing umbone and anterior end. $\times 1.5$.
- 3. YPM 24117, A323, Loc. 28, TLM, Cucullaea AZ; interior. ×1.5.

Fig. 4. Modiolus aff. attenuatus (Meek & Hayden)

4. YPM 24114, A341, Loc. 34, TLM; a poorly preserved specimen. ×1.

Fig. 5. Brachidontes? sp.

5. YPM 24121, A1273, Loc. 170, Colgate lithofacies, ILM; rubber latex cast. ×2.

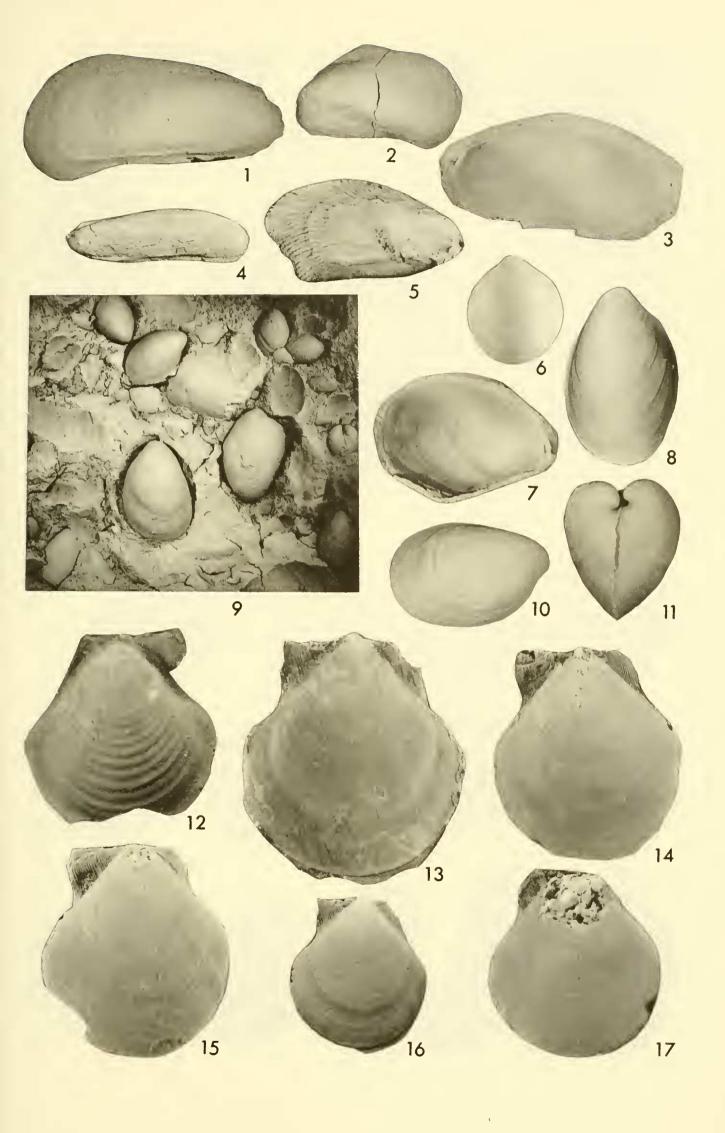
Figs. 6-11. Crenella elegantula Meek & Hayden

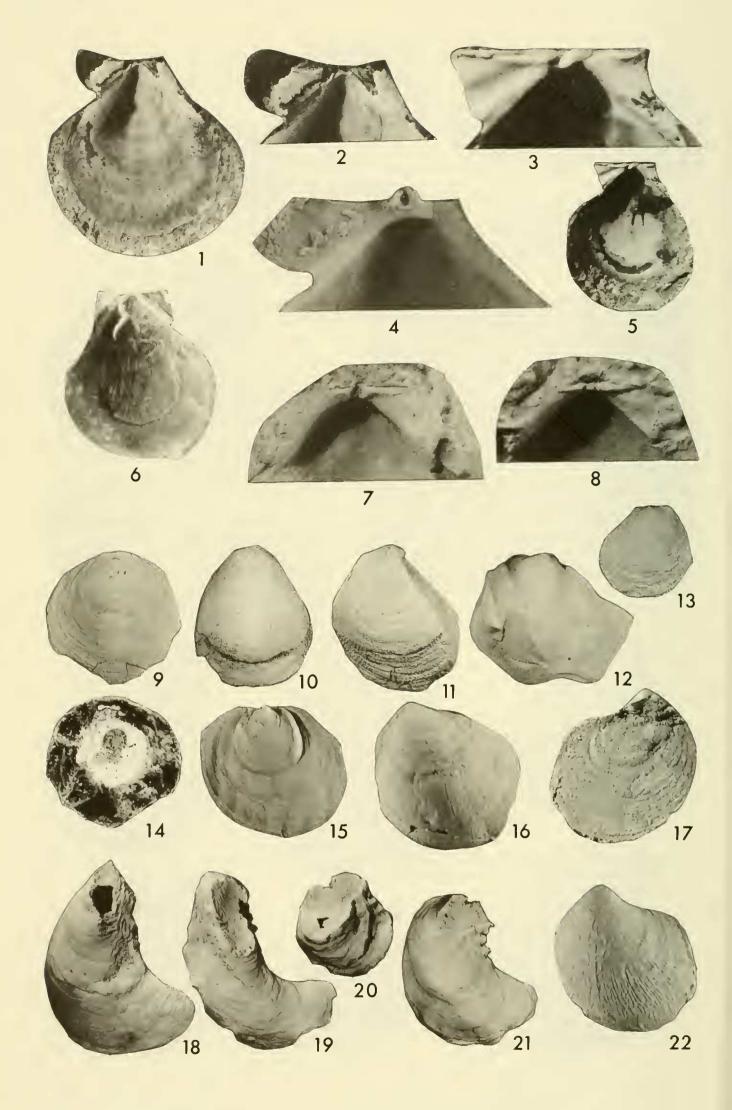
- 6. YPM 24093, A626, Loc. 223, LEl, TCM, Protocardia-Oxytoma AZ; a juvenile specimen with the typical suboval shape. $\times 4$.
- 7. YPM 24092, A419, Loc. 53, LEI, TCM, Lower nicolleti AZ; rubber latex cast showing hinge. $\times 1.5$.
- 8. YPM 24094, A1303, Loc. 177, LEI, TCM, Lower nicolleti AZ. ×2.
- 9. YPM 24091, A547, Loc. 63, LEI, TCM, Lower nicolleti AZ; a surface showing numerous specimens. $\times 1$.
- 10. YPM 24095, A420, Loc. 53, LEI, TCM, Lower nicolleti AZ. ×1.5.
- 11. YPM 24096, A1175, Loc. 120, LEI, TCM, Protocardia-Oxytoma AZ; small muscle insertion on the umbones of the slightly displaced valves of the steinkern. $\times 1.5$.

Figs. 12-17. Syncyclonema halli (Gabb)

- 12. USNM 12272, "Forks of the Cheyenne River, Black Hills, South Dakota"; the original of Plate 7, figure 1 of Whitfield (1880), a right valve steinkern with unusually strong concentric plicae. ×6.
- 13, 16. YPM 24127. ×6.
- 14. YPM 24126. ×6.
- 15. YPM 24129. ×6.
- 17. YPM 24128. $\times 6$.

All from A1409, Loc. 288, TLM, Solen, North Dakota. Notice the very fine "Camptonectes" striae on several of these left valves, particularly on figure 13.





Figs. 1-8. Syncyclonema halli (Gabb)

- 1-2. YPM 24122, A650, Loc. 73, ICl, TCM, Cucullaea AZ; a right valve showing shape, distribution of the white inner layer of the shell, and form of the inner surface of the byssal ear and notch. Fig. 1 ×4; fig. 2 ×6.
- 3-4. YPM 24123, A973, Loc. 100, ICl, TCM, Cucullaea AZ; a right valve showing hinge and inner shell layer (byssal ear incomplete). Fig. 3 × 6; fig. 4 × 12.
- 5. YPM 24125, A747, Loc. 226, TLM, Cucullaea AZ; ventral oblique view of the inner surface of the byssal ear and notch of the right valve, and showing the projecting tooth-like "processes" on either side of the sunken resilifer. ×4.
- 6. ANSP 31241, from the Pierre Shale, Mingusville, Montana, collector Homer Squyer; a right valve steinkern showing pallial line, posteroventral subquadrangular muscle insertion area, and the subcircular insertion area near the base of the posterior ear. ×6.
- 7. USNM 347, "Pierre Shale", Cheyenne and Moreau Rivers, South Dakota; a rubber latex cast of the hinge of a left valve, reputedly the original of Plate 16, figure 5b of Meek (1876). ×6.
- 8. YPM 24124, Loc. 73, ICl, TCM, Cucullaea AZ; hinge of a left valve. ×6.

Figs. 9-17, 22. Anomia gryphorhyncha Meek

- 9, 14. YPM 24104, A725, Loc. 84, Bullhead lithofacies, ILM; showing pattern of muscle insertions on the calcitic plug (14), and elongate resilifer. ×1.
- 10. YPM 24101, A256, Loc. 16, Colgate lithofacies, ILM; a badly worn convex specimen. ×1.
- 11. YPM 24103, A668, Loc. 75, Hell Creek Formation. ×1.
- 12. YPM 24098, A247, Loc. 11, LEI, TCM, Lower nicolleti AZ. ×1.
- 13. YPM 24102, A256, Loc. 16, Colgate lithofacies, ILM. ×1.
- 15. YPM 24100, A545, Loc. 219, LEI, TCM, Lower nicolleti AZ; showing ventral plicae. ×1.
- 16. YPM 24099, A737, Loc. 86, LEI, TCM, Lower nicolleti AZ. X1.
- 17, 22. YPM 24097, A355, Loc. 44, TCM, Lower nicolleti AZ; a bivalved specimen. ×4.

Figs. 18-21. Ostrea translucida Meek & Hayden

- 18. YPM 24723. **★**1.
- 19. YPM 24731. ×1.
- 20. YPM 24735. ×1.
- 21. YPM 24390. $\times 1$.

All from A724, Loc. 83, TLM, Tancredia-Ophiomorpha Biofacies; part of a suite of left valves showing shape variation (see Pl. 19).

Figs. 1-22. Ostrea translucida Meek & Hayden

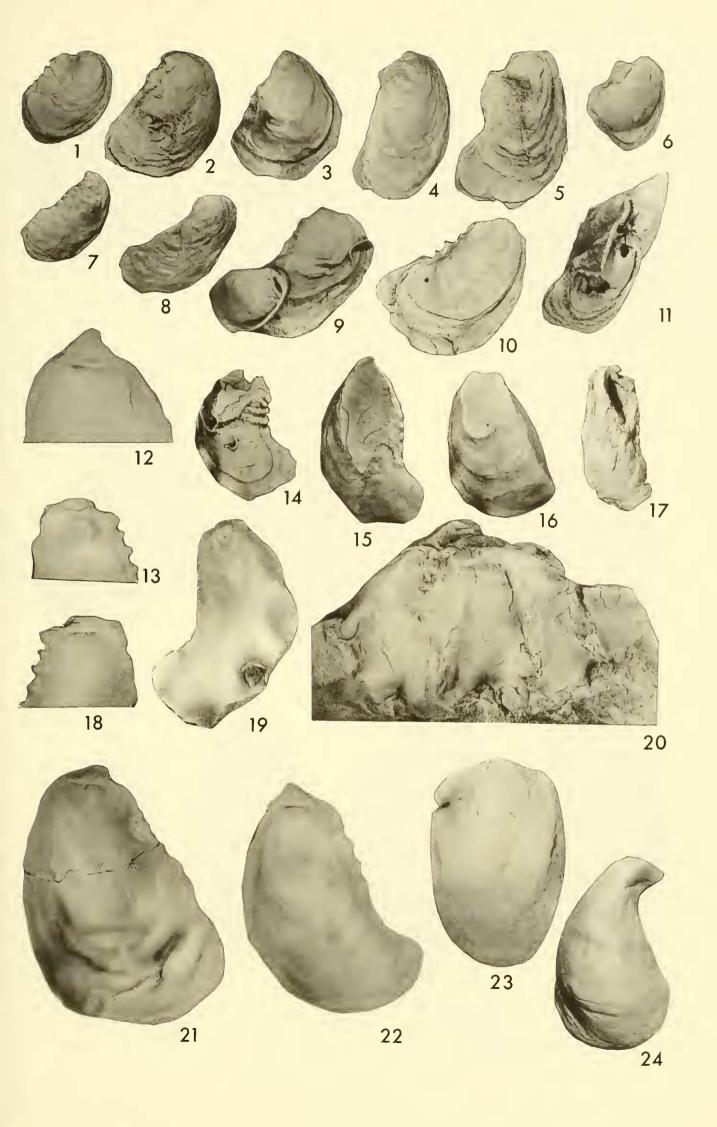
- 1. YPM 24729. ×1.
- 2. YPM 24732. ×1.
- 3. YPM 24728. ×1.
- 4. YPM 24724. ×1.
- 5. YPM 24722. ×1.
- 6. YPM 24734. ×1.
- 7. YPM 24726. ×1.
- 7. IIW 24720. A1.
- 8. YPM 24737. ×1.
- 9. YPM 24727. ×1.
- 10. YPM 24387. $\times 1$.
- 11. YPM 24733. ×1.
- 12. YPM 24391. ×2.
- 13, 18. YPM 24389. ×2.
- 14. YPM 24725. ×1.
- 15. YPM 24736. **★**1.
- 16. YPM 24730. ×1.
- 17. YPM 24392. $\times 1$.
- 19. YPM 24393, A652, Loc. 73, ICl, TCM, Cucullaea AZ; a specimen with a strongly plicate anteroventral margin. ×1.
- 20. YPM 24394, A337, Loc. 33, TLM; a cluster of specimens attached to a stem. ×1.
- 21. YPM 24388. ×1.5.
- 22. YPM 24386. ×1.5.

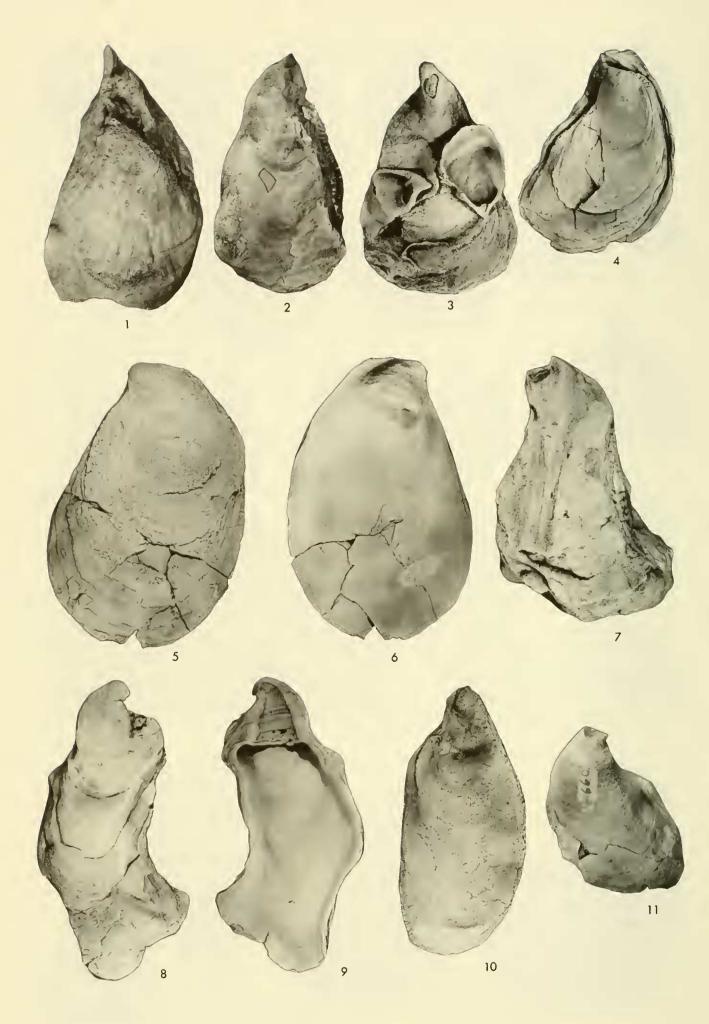
All except figures 19 and 20 from A724, Loc. 83, TLM, Tancredia-Ophiomorpha Biofacies. Exterior views showing shape, marginal plications, attachment areas, and epizoans (small spat); and internal views showing muscle insertion areas, and the denticles and matching sockets on the dorsal margins of the right and left valves respectively.

Figs. 23, 24. Crassostrea subtrigonalis (Evans & Shumard)

- 23. YPM 24418. ×1.
- 24. YPM 24718. ×1.

Both from A256, Loc. 16, Colgate lithofacies, ILM. Specimens differing greatly in shape.





Figs. 1-11. Crassostrea subtrigonalis (Evans & Shumard)

- YPM 24720, A256, Loc. 16; showing strong radial costae.
- YPM 24721, A256, Loc. 16. 2.
- YPM 24719, A256, Loc. 16. YPM 24417, A647, Loc. 72. 3.
- 4.
- 5-6. YPM 24421, A926, Loc. 84; shell with borings resembling those made by clioniid sponges.
- 7. YPM 24717, A256, Loc. 16; specimen with a very large attachment area (to wood).
- 8-9. YPM 24422, A256, Loc. 16.
- YPM 24420, A926, Loc. 84; shell with borings resembling those made by clioniid sponges.
- 11. YPM 24419, A660, Loc. 74.

All from Colgate lithofacies, ILM, and all $\times 0.67$.

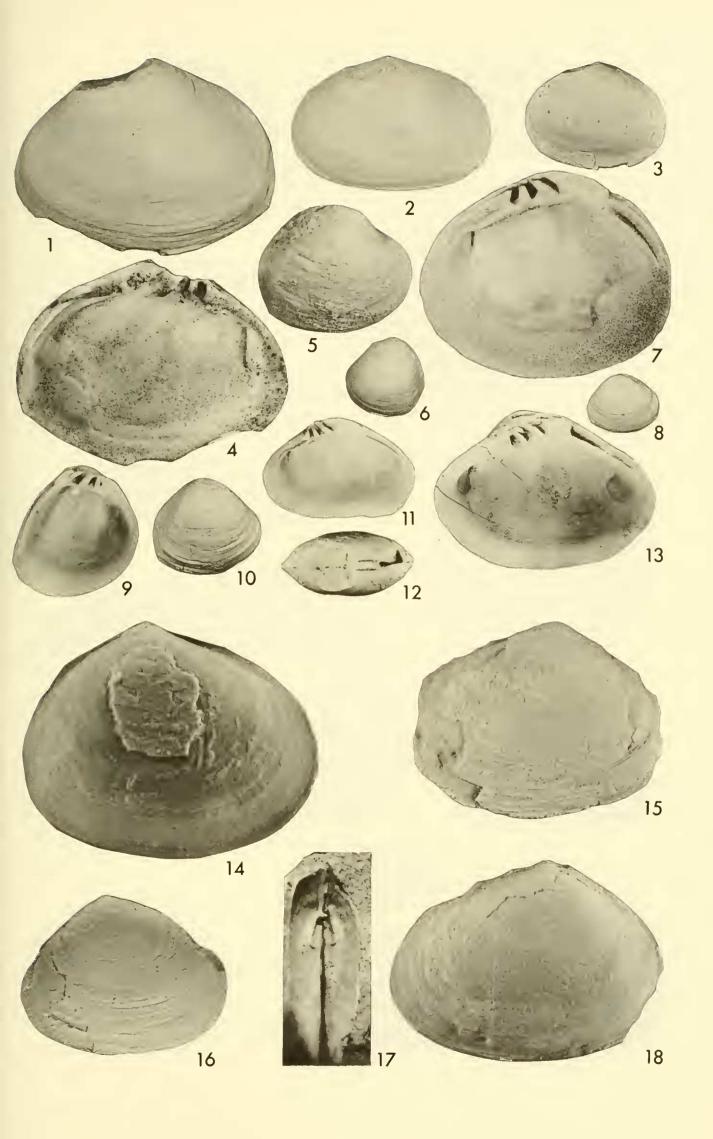
Figs. 1-13. Corbicula sp. A.

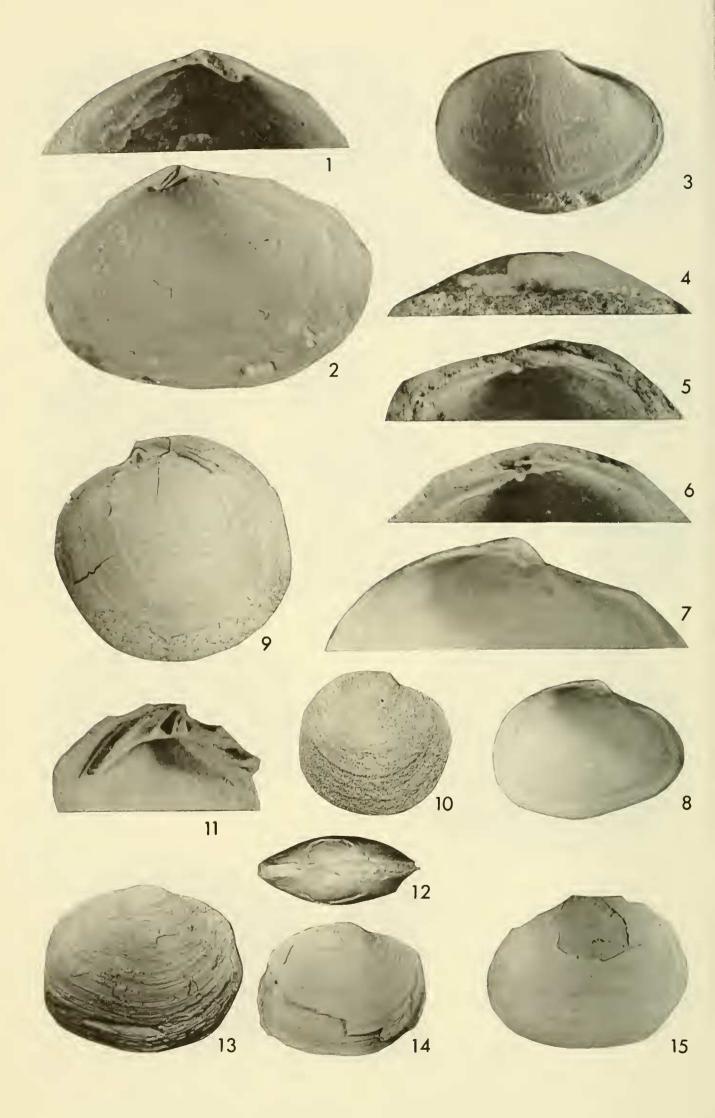
- 1, 4. YPM 24395, A660, Loc. 74; oval form. ×2.
- YPM 24398, A256, Loc. 16; compressed elliptical form. ×2.
- YPM 24396, A660, Loc. 74; oval form. ×2.
- YPM 24399, A299, Loc. 264; oval form. ×1. 5.
- YPM 24713, A299, Loc. 264; oval form. ×1. 6.
- YPM 24401, A256, Loc. 16, oval form. $\times 2$. 7.
- YPM 24712, A299, Loc. 264, oval form. ×1. 8.
- 9. YPM 23874, A256, Loc. 16, a high oval form. $\times 1$.
- YPM 24714, A299, Loc. 264; oval form. ×1. 10.
- YPM 23879, A299, Loc. 264; compressed form. $\times 1$. 11.
- YPM 24396, A660, Loc. 74; oval form. $\times 2$. 12.
- YPM 23878, A299, Loc. 264; a large specimen tending to elongate and compress with 13. increasing size. $\times 1$.

All from the Colgate lithofacies, ILM.

Figs. 14-18. Spaniorinus nicolleti Speden, sp. n.

- 14. YPM 24404, A981, Loc. 102, LEI, TCM, Protocardia-Oxytoma AZ; a steinkern showing faint adductor insertion areas and pallial line. $\times 6$.
- YPM 24403, A578, Loc. 191, LEI, TCM, Protocardia-Oxytoma AZ. ×6. YPM 24407, A623, Loc. 222, LEI, TCM, Lower nicolleti AZ. ×6. 15.
- 16.
- YPM 24406, A1342, Loc. 253, LEI, TCM, Protocardia-Oxytoma AZ; showing the in-17. terior of the umbonal region, and resilifer plates and teeth. ×6.
- YPM 24405, A1046, Loc. 238, LEI, TCM, Protocardia-Oxytoma AZ; holotype. ×6. 18.





Figs. 1-2. Spaniorinus nicolleti Speden, sp. n.

- 1. YPM 24408, A704, Loc. 206, LEl, TCM, Lower *nicolleti* AZ; rubber latex cast of right valve hinge. ×6.
- 2. YPM 24409, A531, Loc. 218, LEI, TCM, Lower nicolleti AZ; rubber latex cast of left valve hinge. ×6.

Figs. 3-8. Hindsiella corsonensis Speden, sp. n.

- 3. YPM 24415, A617, Loc. 221, LEI, TCM, Limopsis-Pseudoptera AZ; note the weakly impressed adductor insertion areas and pallial line. ×6.
- 4. YPM 24414, A623, Loc. 222, LEl, TCM, Lower *nicolleti* AZ; dorsal view of right valve holotype. ×9.
- 5. YPM 24413, A1160, Loc. 118, LEl, TCM, Lower nicolleti AZ; right valve hinge showing the strongly projecting cylindrical tooth. ×9.
- 6. YPM 24412, A1106, Loc. 249, LEl, TCM, Lower *nicolleti* AZ; right valve hinge showing the strongly projecting tooth. ×9.
- 7-8. YPM 24416, A967, Loc. 100, ICl, TCM, Cucullaea AZ; left valve hinge; faintly impressed anterior adductor insertion area visible on figure 8. Fig. 7 × 9; fig. 8 × 6.

Figs. 9-11. Epilucina cedrensis (Stanton)

9–10. YPM 24436. Fig. 9 \times 1.5; fig. 10 \times 1.

11. YPM 24435. $\times 3$.

Both from A724, Loc. 83, TLM, Tancredia-Ophiomorpha Biofacies; showing hinges and muscle insertion areas.

Figs. 12-14. Nymphalucina occidentalis (Morton)

- 12, 14. YPM 24424, A928, Loc. 95, LEI, TCM, Protocardia-Oxytoma AZ; lateral and dorsal views, with ligament preserved. Fig. 12 ×1.
- 13. YPM 24427, A241, Loc. 10, LEI, TCM, Limopsis-Pseudoptera AZ. ×1.

Fig. 15. Erycina? sp. A

15. YPM 24411, A1297, Loc. 176, LEI, TCM, abyssinus concretion; a left valve. ×6.

Figs. 1-7, 10-13. Nymphalucina occidentalis (Morton)

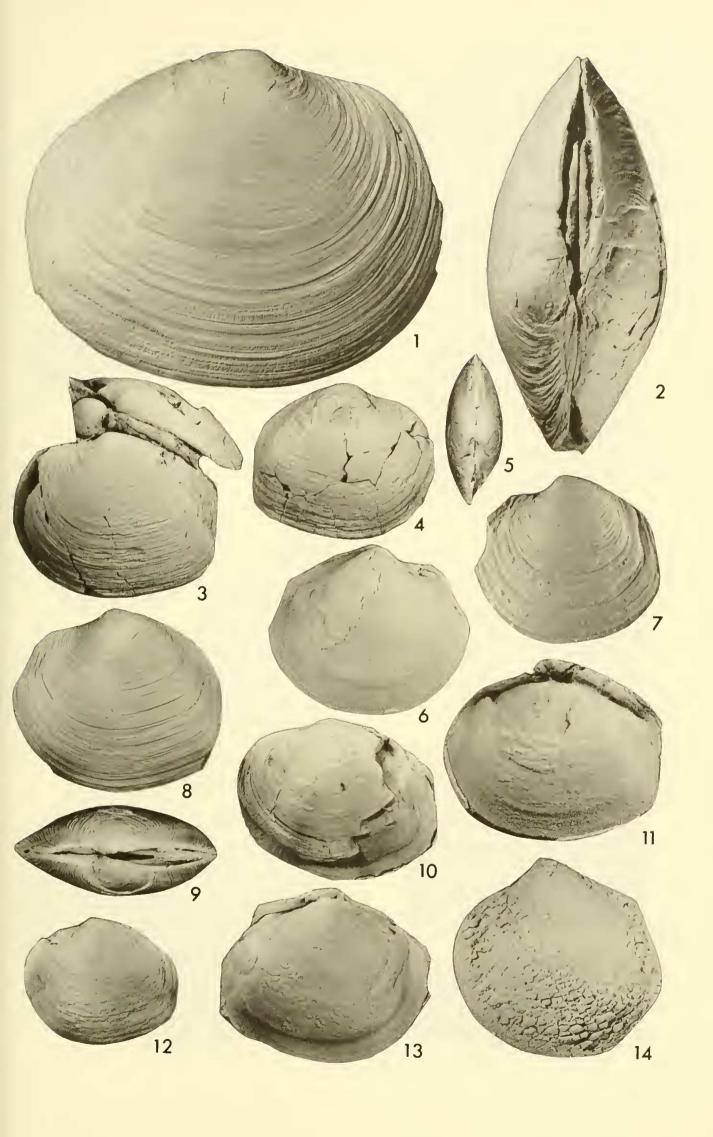
- 1-2. USNM 334, from "near mouth of Milk River, Montana, Pierre Shale"; the original of figures 4a, b of Meek (1876, Pl. 17). ×2.
- 3. YPM 24433, A1216, Loc. 138, LEl, TCM, Protocardia-Oxytoma AZ; showing ligament articulating the two valves. ×1.
- 4. YPM 24432, A693, Loc. 204, LEI, TCM, Limopsis-Pseudoptera AZ; ×1.
- 5, 12. YPM 24426, A930, Loc. 95, LEI, TCM, Limposis-Pseudoptera AZ; ligament preserved.
- 6. YPM 24639, A1260, Loc. 161, ICl, TCM, Protocardia-Oxytoma AZ. ×2.
- 7. YPM 24428, A787, Loc. 90, TLM, Sphenodiscus layer; a juvenile specimen. ×4.
- 10. YPM 24640, A1215, Loc. 138, LEI, TCM, Protocardia-Oxytoma AZ; showing posterior muscle insertion and ventral costae on the inner shell surface (negative on the steinkern). ×1.
- 11. YPM 24425, A603, Loc. 66, LEl, TCM, Lower nicolleti AZ; a small subquadrate-shaped specimen. ×2.
- 13. YPM 24431, A226, Loc. 8, LEI, TCM, Limopsis-Pseudoptera AZ; showing nymph, and muscle insertion areas, pallial line and trace of the pallial blood vessel on the steinkern. ×1.

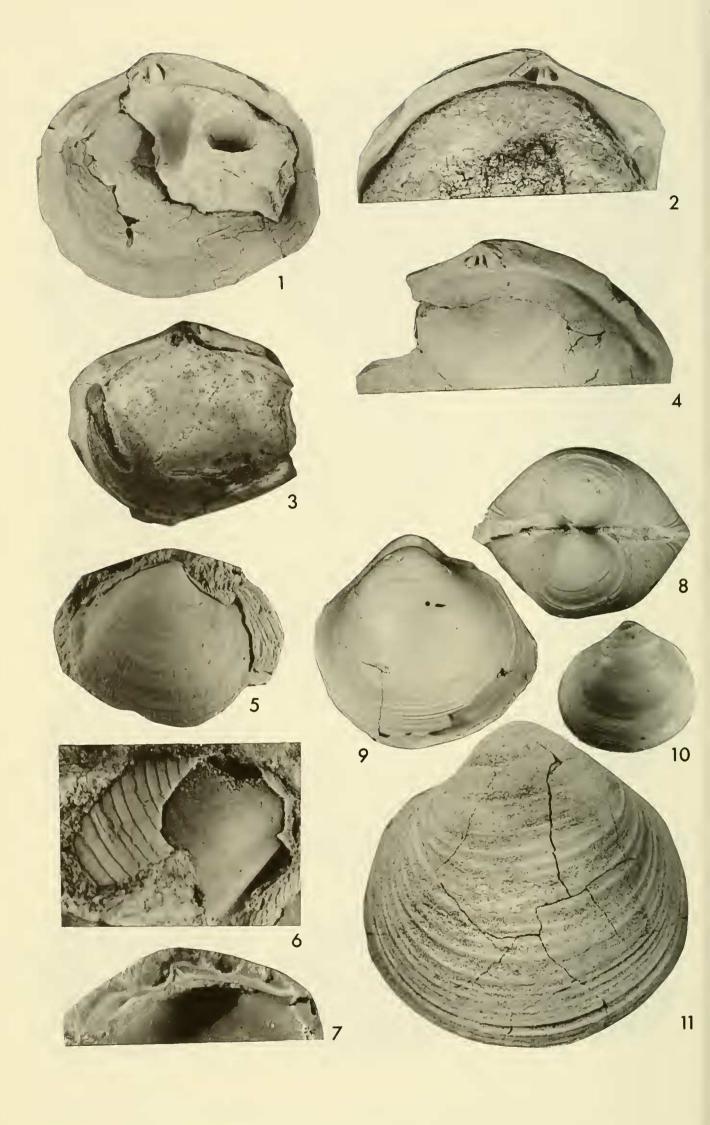
Figs. 8-9. Nymphalucina "cleburni" (White)

8, 9. YPM 24641, "Platte River Valley, N.E. Colorado, Upper Cretaceous, Gordon Collection," on the accompanying label; specimen shows the fine projecting costae apparently characteristic of this species. ×1.

Fig. 14. Lucina? sp. indet.

14. YPM 24423, A510, Loc. 215, Elk Butte Member, Pierre Shale. ×2.





Figs. 1-2, 4-7. Nymphalucina occidentalis (Morton)

- 1. YPM 24432, A693, Loc. 204, LEI, TCM, Limopsis-Pseudoptera AZ; showing hinge and nymph. ×1.5.
- 2, 4. YPM 24434, A690, Loc. 204, LEI, TCM, Limopsis-Pseudoptera AZ; matching hinges; notice the small secondary teeth (vincula) in the sockets in figure 4. ×1.5.
- 5-6. YPM 24429, A789, Loc. 90, TLM, Cucullaea AZ; a small specimen with projecting plates along the dorsal margins and arched flanges on the costae (evident as extensions into the matrix on fig. 6). Fig. 5 ×6; fig. 6 ×8.
- 7. YPM 24430, A791, Loc. 90, TLM, Sphenodiscus layer; a rubber latex cast of the hinge of a juvenile specimen. ×4.

Fig. 3. Nymphalucina "cleburni" (White)

3. YPM 24642. "Platte River Valley, N.E. Colorado, Upper Cretaceous, Gordon Collection" on the associated label; showing hinge, anterior adductor insertion area, and the reflexed pallial blood vessel impression. ×1.5.

Figs. 8-11. Clisocolus moreauensis (Meek & Hayden)

- 8-9. YPM 24015, A701, Loc. 206, LEI, TCM, Lower nicolleti AZ. ×1.
- 10. YPM 24018, A998, Loc. 232, LEI, TCM, Lower nicolleti AZ; a very small specimen showing widely spaced fine radial markings, color banding, and fine concentric costae, ×8.
- 11. GSC type No. 20196, GSC Loc. 23726, Halfbreed Creek, Alberta, Pakowki Formation, Bear Gulch Sandstone Lentil, R. W. Landes, Collector. ×2.

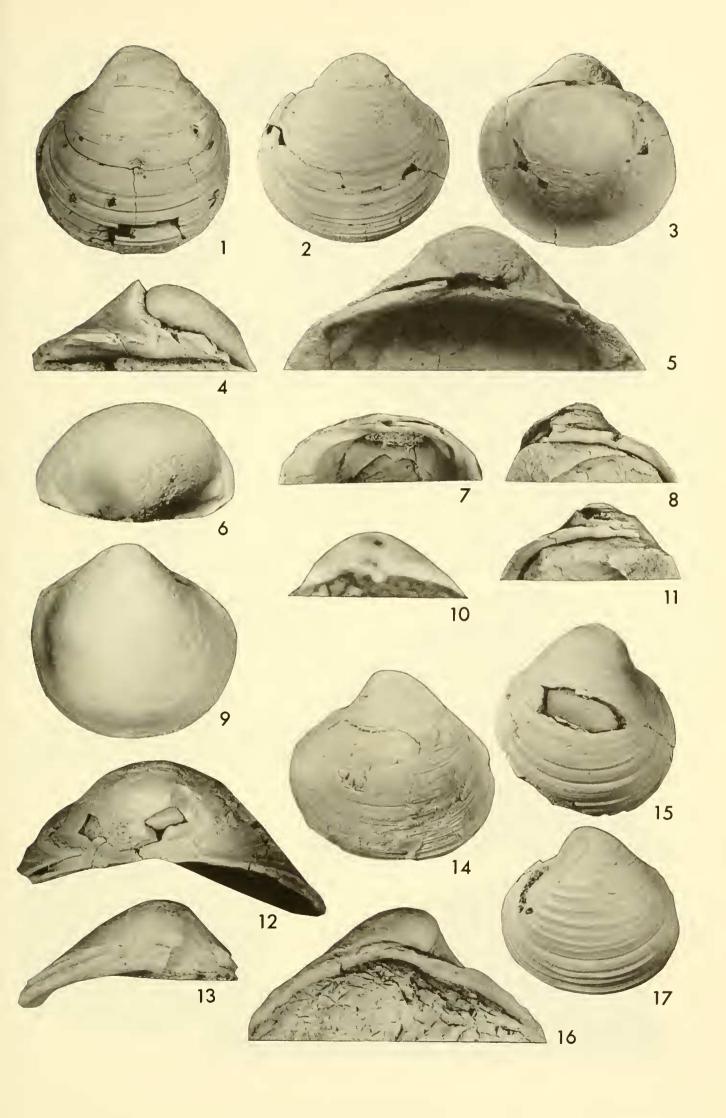
Figs. 1-13. Clisocolus moreauensis (Meek & Hayden)

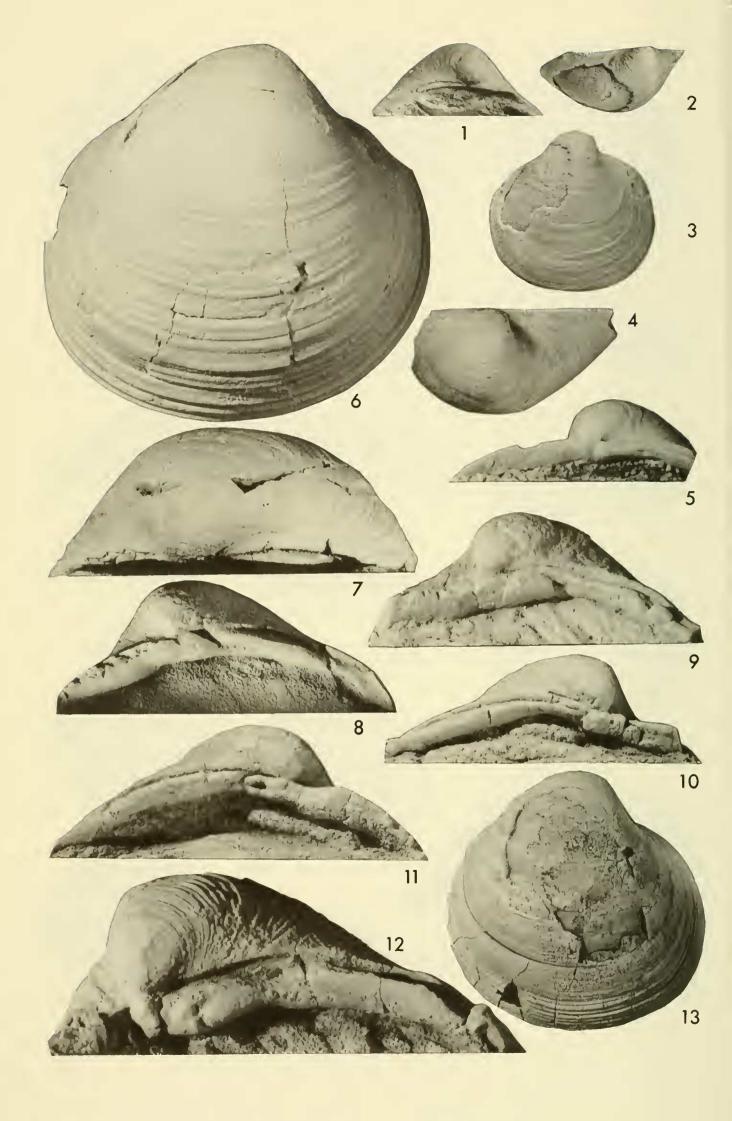
- 1. YPM 24016, A1170, Loc. 110, LEI, TCM, Protocardia-Oxytoma AZ; a specimen with height greater than length. ×1.
- 2, 3, 5. GSC cat. type No. 20194, GSC Loc. 23725, Pakowki Formation, Bear Gulch Sandstone Lentil, Alberta, R. W. Landes, Collector; Upper Campanian; specimen showing hinge and projections on the inner surface of the shell. Note the deep impressions of the pedal muscle insertions on figure 5. Figs. 2, 3, ×1; fig. 5 ×2.
- 4. YPM 24014, A1008, Loc. 233, LEl, TCM, Protocardia-Oxytoma AZ; showing the projection on the dorsal margin above the cardinal protuberance. ×2.
- 6, 9. YPM 24017, A268, Loc. 21, TCM, LEI, Lower nicolleti AZ; steinkern showing adductor and pedal muscle insertions, and pallial line. ×1.
- 7. YPM 24009, A433, Loc. 54, LEl, TCM, Lower nicolleti AZ; rubber latex cast of right valve hinge showing hinge, strong nymph, and the pit for the inner ligament and associated groove crossing the anterior end of the nymph. ×1.
- 8, 11. YPM 24010, A1300, Loc. 177, LEI, TCM, Lower nicolleti AZ; the anterior part of matching hinges showing a cardinal protuberance on the left valve, and a strong posterior and a weak anterior protuberance on the right valve. ×1.
- 10. YPM 24019, A623, Loc. 222, LEI, TCM, Lower *nicolleti* AZ; a small left valve showing nymph and two cardinal teeth (the upper surface of teeth broken off). ×12.
- 12. YPM 24011, A1231, Loc. 143, LEl, TCM, Protocardia-Oxytoma AZ; a specimen with umbone and center of hinge eroded away during life. ×2.
- 13. YPM 24012, A1361, Loc. 258, LEI, TCM, Lower nicolleti AZ; posterior part of a left valve hinge showing strong nymph and the pit for inner ligament. ×2.

Figs. 14-17. Clisocolus dubius (Gabb) (The cordatus Whiteaves of authors)

- 14, 16. UCLA Cat. No. 34131, Loc. 453. Fig. 14 ×1; fig. 16 ×1.5.
- 15. CIT 975. $\times 1$.
- 17. CIT 974; outer shell worn off. ×1.

 All collected by W. P. Popenoe, from the Pleasants Sandstone Formation, Upper Campanian, Santa Ana Mountains, California.





Figs. 1-5, 13. Clisocolus dubius (Gabb) (The cordatus Whiteaves of authors)

- 1. CIT 39475. $\times 2$.
- 2-3. CIT 39476. ×2.

Both specimens from CIT Loc. 1400, Cedar District Formation, Upper Campanian, Sucia Island, British Columbia, Canada; showing fine concentric costae on umbones and shell; compare with figures 4, 5.

- 4-5. ANSP 4403, Texas Flat, California, Lower Asuncion Group, lower-middle Campanian; holotype, showing hinge and fine concentric costae on the umbone. Fig. 4 ×4; fig. 5 ×6.
- 13. UCLA Cat. No. 34130, Loc. 2415, Bee Canyon, Santa Ana Mountains, Pleasants Sandstone Formation, Upper Campanian. ×1.

Figs. 6-8. Clisocolus moreauensis (Meek & Hayden)

6-8. USNM 21876, 4 miles north of Colorado Springs, Colorado, Fox Hills Formation; showing ornament, strong nymph, and deep pit for the inner ligament. ×2.

Figs. 9-12. Clisocolus corrugatus Popenoe

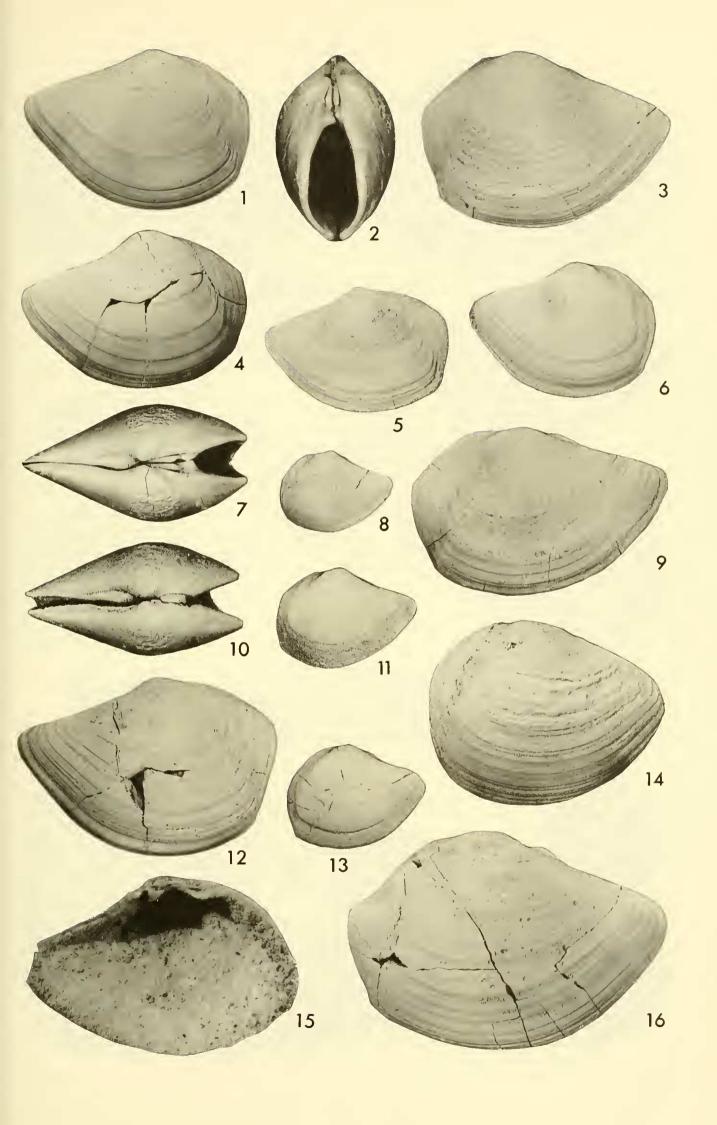
- 9. UCLA 39599, Loc. 170. ×4.
- 10. UCLA 39598, Loc. 1069. ×4.
- 11. UCLA 39596, Loc. 1068. ×4.
- 12. UCLA 39597, Loc. 1069. ×4.

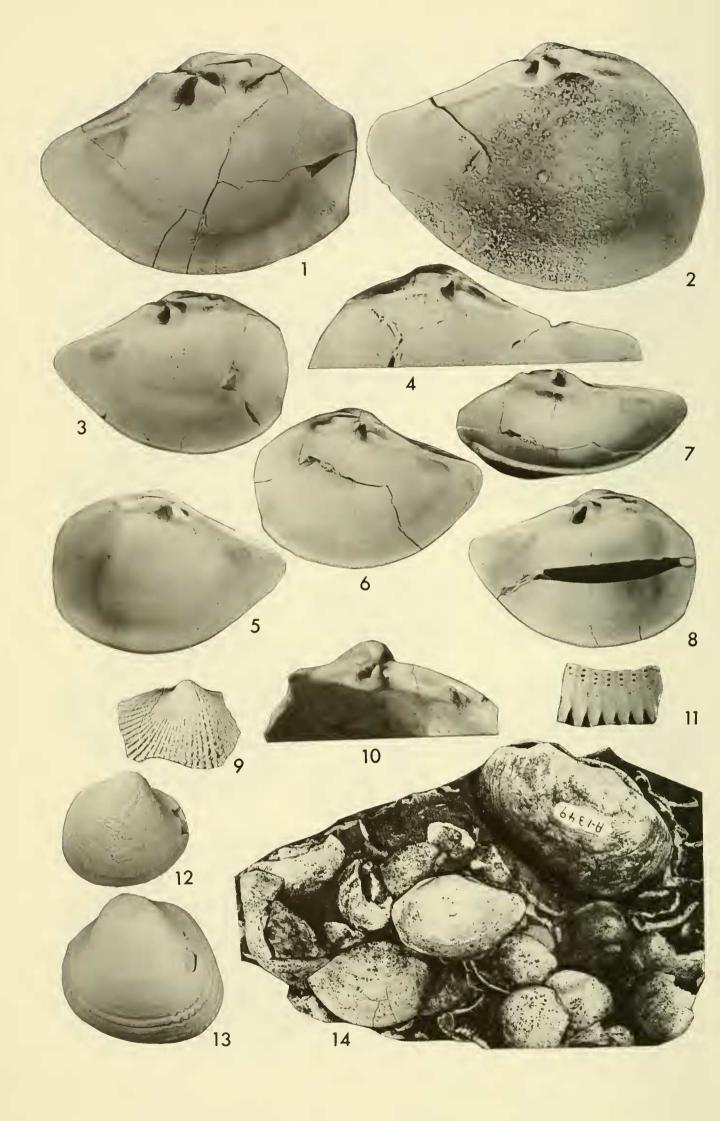
All from the Santa Ana Mountains, California, Baker Canyon Sandstone, Turonian; showing hinges with resilifer pits (for the inner ligament) of different sizes and degree of depression.

Figs. 1-16. Tancredia americana (Meek & Hayden)

- 1–2. YPM 24382, A370, Loc. 48. ×1.
- 3. YPM 24703, A724, Loc. 83. ×1.
- 4, 7. YPM 24383, A288, Loc. 85. ×1.
- 5. YPM 24706, A724, Loc. 83. ×1.
- 6. YPM 24704, A724, Loc. 83. ×1.
- 8. YPM 24381, A724, Loc. 83. ×1.
- 9. YPM 24705, A724, Loc. 83. ×1.
- 10. YPM 24378, A724, Loc. 83; valves slightly displaced. ×1.
- 11. YPM 24701, A724, Loc. 83. ×1.
- 12. YPM 24702, A724, Loc. 83. ×1.
- 13. YPM 24699, A724, Loc. 83. ×1.
- 14. YPM 24379, A290, Loc. 207. ×1.
- 15. YPM 24380, A724, Loc. 83; hinge of very small specimen. ×4.
- 16. YPM 24385, A370, Loc. 48. ×1.

All from TLM, Tancredia-Ophiomorpha Biofacies. Notice the variation of shape, wide posterior gape, and strength of nymphs.





Figs. 1-8, 14. Tancredia americana (Meek & Hayden)

- 1. YPM 24385, A370, Loc. 48. ×1.
- 2. YPM 24381, A724, Loc. 83. ×2.
- 3, 5. YPM 24382, A370, Loc. 48. ×1.
- 4. YPM 24381, A724, Loc. 83. ×2.
- 6, 7, 8. YPM 24383, A288, Loc. 25; showing pedal muscle insertion areas (fig. 7) and a vincula pad on the posterior cardinal of the left valve. ×1.
- 14. YPM 24172, A1349, Loc. 254; a block from a shellbed, showing valves oriented mainly concave down, and with a specimen of *Panopea occidentalis* Meek & Hayden. ×0.5.

All from the TLM, Tancredia-Ophiomorpha Biofacies.

Figs. 9-11. Granocardium (Ethmocardium) aff. whitei (Dall)

9-11. YPM 24180, A667, Loc. 224, Bullhead Member. Fig. 9, 11 ×4; fig. 10 ×8.

Figs. 12-13. Protocardia subquadrata (Evans & Shumard)

- 12. YPM 24198, A362, Loc. 46, LEI, TCM, Lower nicolleti AZ; the largest specimen collected. ×1.
- 13. YPM 24200, A669, Loc. 195, TLM, Cucullaea AZ; showing the sharp appearance of radial costae. ×4.

Figs. 1-16. Protocardia subquadrata (Evans & Shumard)

YPM 24649, A478, Loc. 212, ICl, TCM, Cucullaea AZ; a specimen with ligament preserved. Fig. 1 \times 2; fig. 4 \times 3.

YPM 24190, A480, Loc. 212, ICl, TCM, Cymbophora-Tellinimera AZ. ×2. 2.

YPM 24192, A441, Loc. 56, ICl, TCM, Cucullaea AZ. ×2. 3.

YPM 24191, A798, Loc. 92, ICl, TCM, Cucullaea AZ; notice the posterodorsal margin 5, 6. of the right valve overlapping the margin of the left valve, and the variation in the strength and the point of appearance of the radial costae on the external shell. Fig. 5 \times 6; fig. 6 \times 4.

YPM 24185, A798, Loc. 92; showing a discontinuous pallial line and posterior pedal re-7.

tractor insertion. $\times 9$.

YPM 24377, A921, Loc. 92; showing dorsal margin and the upper surface of the 8. nymph. $\times 4$.

YPM 24376, A921, Loc. 92; a gaping specimen retaining ligament. ×4. 9.

10. YPM 24184, A798, Loc. 92. ×9.

YPM 24188, A798, Loc. 92; showing an irregular pallial line. ×9. 11.

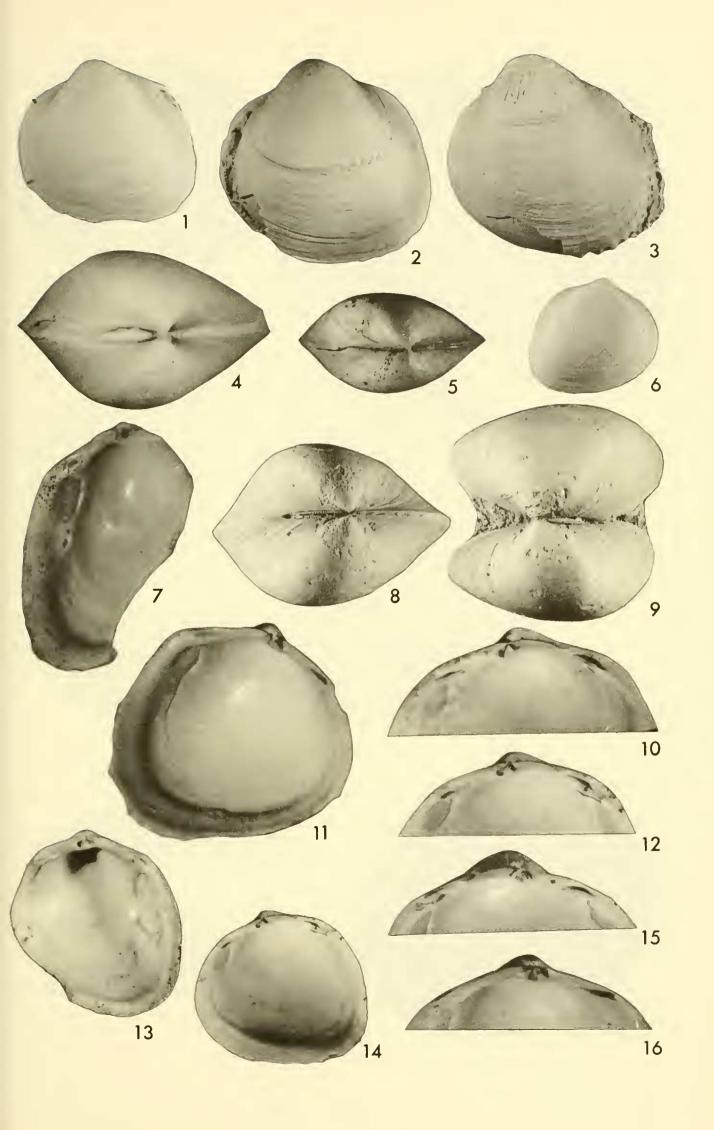
12, 14. YPM 24189, A798, Loc. 92. ×9.

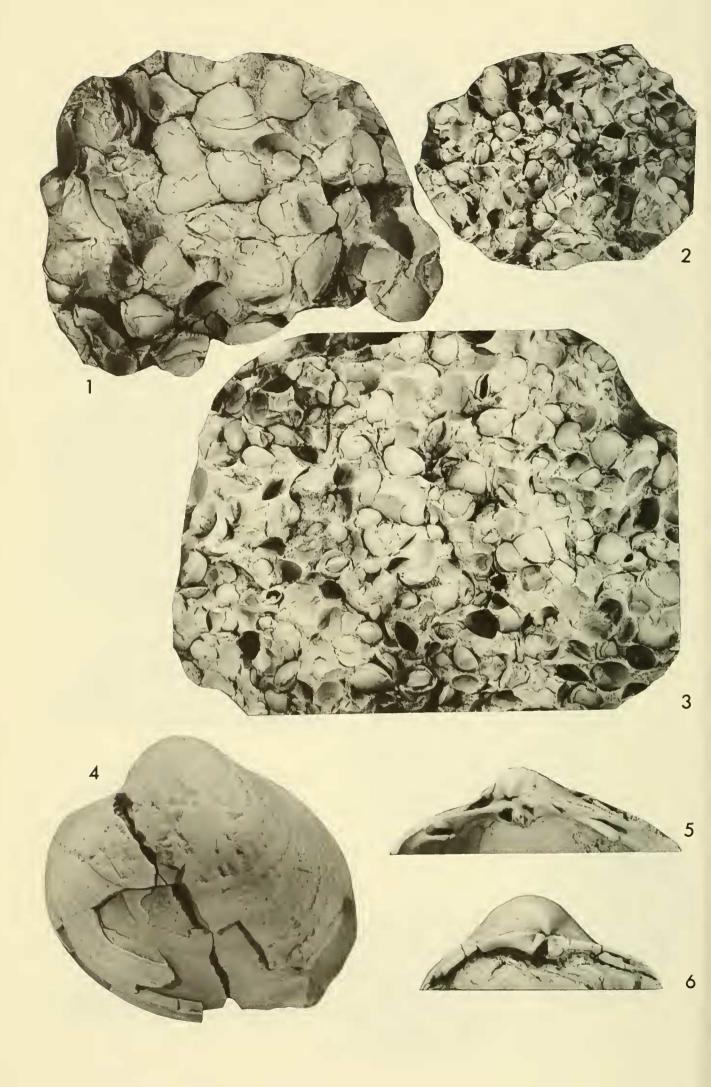
YPM 24477, A798, Loc. 92; showing the normal pallial line with three sinuses. ×9. YPM 24187, A798, Loc. 92. ×9. 13.

15.

16. YPM 24186, A798, Loc. 92. ×9.

All specimens figures 7-16 from ICl, TCM, Cucullaea AZ.





Figs. 1-3. Protocardia subquadrata (Evans & Shumard)

- 1. YPM 24197, A1276, Loc. 173, LEI, TCM, Protocardia-Oxytoma AZ. ×1.
- 2. YPM 24195, A577, Loc. 191, LEI, TCM, Protocardia-Oxytoma AZ. ×1.
 3. YPM 24194, A1137, Loc. 113, TLM, Cucullaea AZ. ×1. Three blocks from different concretions, each block containing a limited size class of specimens.

Figs. 4-6. Protocardia sp.

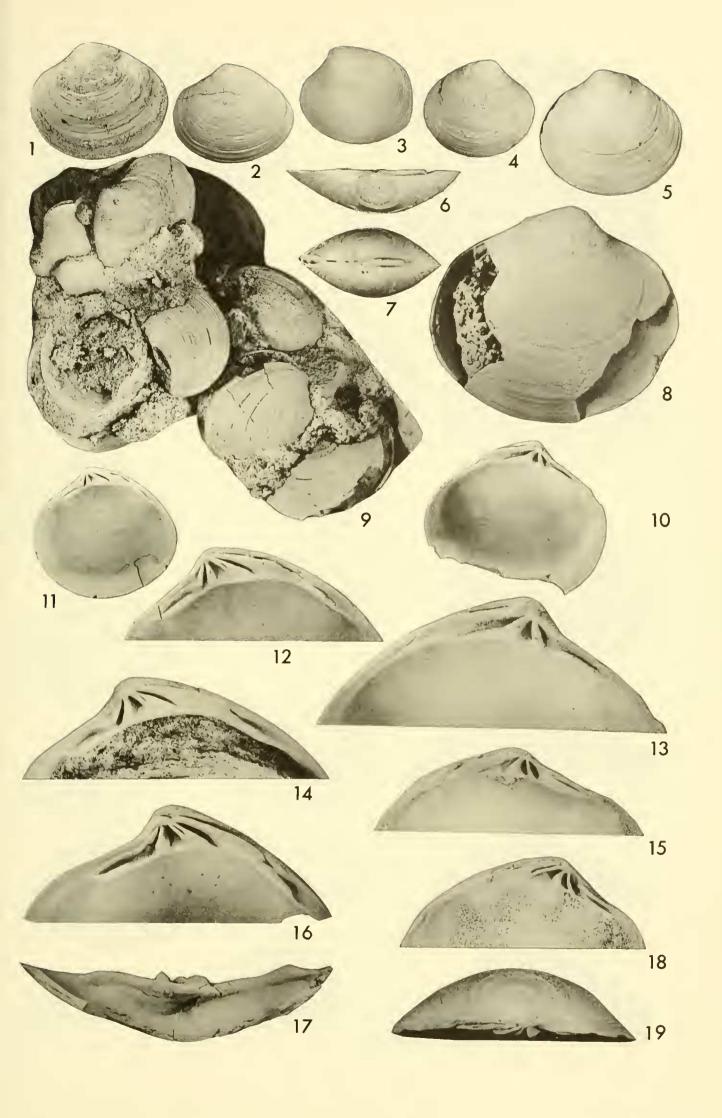
- 4. YPM 24183, A1303, Loc. 177. ×1.
- 5. YPM 24181, A530, Loc. 218; rubber latex cast. ×1.
- 6. YPM 24182, A372, Loc. 46. ×1.

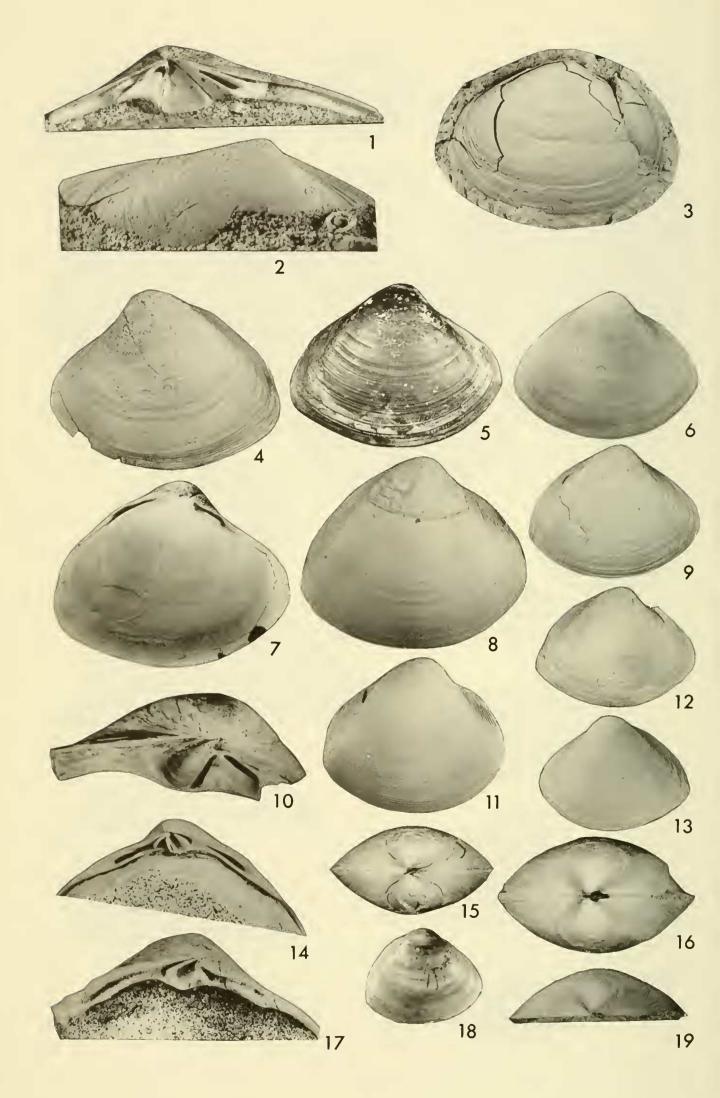
All from LEI, TCM, Lower nicolleti AZ.

Figs. 1-19. Dosiniopsis deweyi (Meek & Hayden)

- 1. YPM 24708, A1316, Loc. 183. ×1.
- 2. YPM 24710, A1316, Loc. 183. ×1.
- 3. YPM 24170, A348, Loc. 37, TLM, Cucullaea AZ. ×1.
- 4. YPM 24711, A1316, Loc. 183 (the posterodorsal margin of this specimen was subsequently partly destroyed). ×1.
- 5, 7. YPM 24174, A1395, Loc. 194. ×1.
- 6, 10, 13. YPM 24178, A724, Loc. 83. The tips of the cardinal teeth are incomplete. Figs. 6, 10×1 ; fig. 13 $\times 2$.
- 8. YPM 24169, A972, Loc. 100, ICl, TCM, Cucullaea AZ. ×2.
- 9. YPM 24171, A1316, Loc. 183; a cluster of specimens. $\times 1$.
- 11, 12. YPM 24177, A724, Loc. 83. Fig. 11 \times 1; fig. 12 \times 2.
- 14. YPM 24173, A1208, Loc. 135. ×2.
- 15. YPM 24175, A1330, Loc. 190. ×2.
- 16, 17. YPM 24176, A724, Loc. 83; showing hinge and pedal muscle insertions (shell subsequently fractured damaging the ventral part of the hinge under the posterior cardinal tooth. Compare figure 17 with figure 16). ×2.
- 18, 19. YPM 24179, A1316, Loc. 183. ×2.

All from TLM, Tancredia-Ophiomorpha Biofacies, except where noted otherwise.





Figs. 1-3. Spisula? sp. indet.

- YPM 24438, A667, Loc. 224, Bullhead lithofacies, ILM. ×4.
- YPM 24439, A661, Loc. 74, Bullhead lithofacies, ILM. ×1.5.

Figs. 4-19. Cymbophora warrenana (Meek & Hayden)

- YPM 24445, A724, Loc. 83, TLM, Tancredia-Ophiomorpha Biofacies; showing the 4, 7. projections along the dorsal margin of the pallial line. $\times 1$.
- 5.
- YPM 24444, A1322, Loc. 184, TLM, Cucullaea AZ. ×1.
 YPM 24446, A1192, Loc. 130, ICl, TCM, Cymbophora-Tellinimera AZ. ×1.
 YPM 24441, A504, Loc. 60, TLM, Cymbophora-Tellinimera AZ. ×2. 6.
- 8.
- 9. YPM 24451, A1268, Loc. 163, TLM, Cucullaea AZ. ×1.
- 10. YPM 24448, A446, Loc. 56, Bullhead lithofacies, ILM. ×4.
- 11. YPM 24440, A505, Loc. 60, TLM, Cymbophora-Tellinimera AZ. ×2.
- 12. YPM 24450, A1268, Loc. 163, TLM, Cucullaea AZ. ×1.
- 13. YPM 24442, A441, Loc. 56, ICl, TCM, Cymbophora-Tellinimera AZ. ×1.
- 14, 19. YPM 24446, A1192, Loc. 130, ICl, TCM, Cymbophora-Tellinimera AZ. Fig. 14 ×1.5; Fig. 19 \times 1.
- 15. YPM 24451, A1268, Loc. 163, TLM, Cucullaea AZ. ×1.
- 16. YPM 24449, A1207, Loc. 133, ICl, TCM. ×1.
- 17.
- YPM 24447, A724, Loc. 83, TLM, Tancredia-Ophiomorpha Biofacies. ×1.5. YPM 24443, A480, Loc. 212, ICl, TCM, Cymbophora-Tellinimera AZ; a juvenile 18. specimen showing color banding. ×4.

Fig. 1. Cymbophora? nitidula (Meek & Hayden)

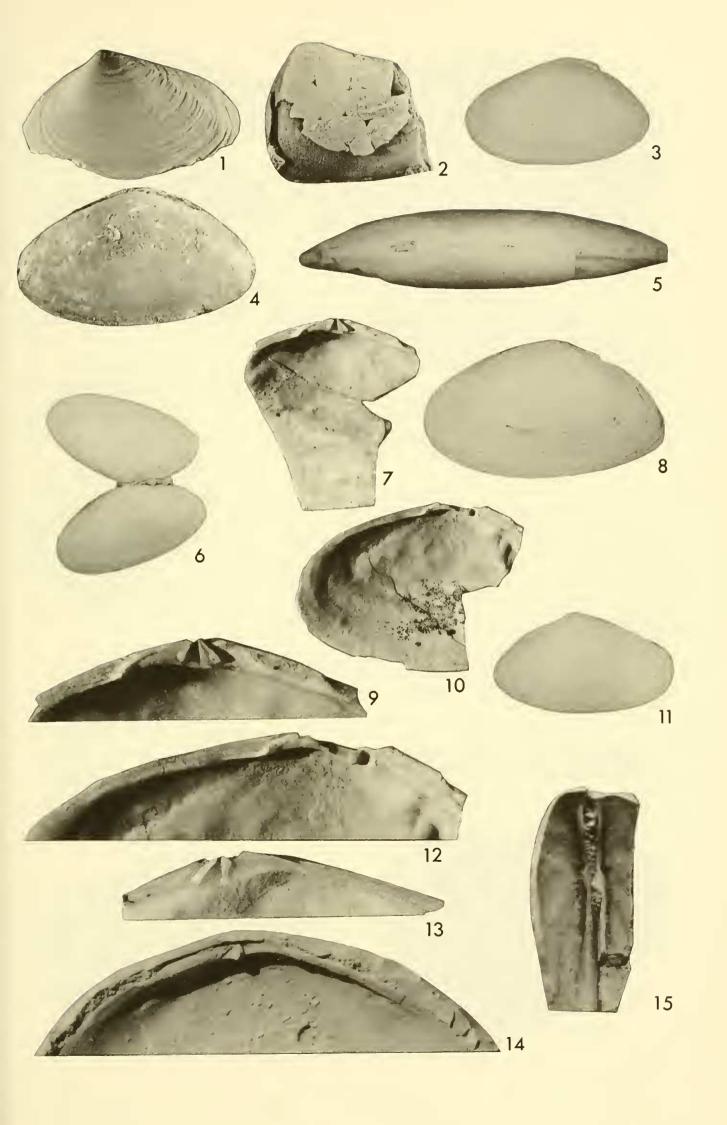
1. YPM 24437, A457, Loc. 210, ICl, TCM, Cymbophora-Tellinimera AZ. ×4.

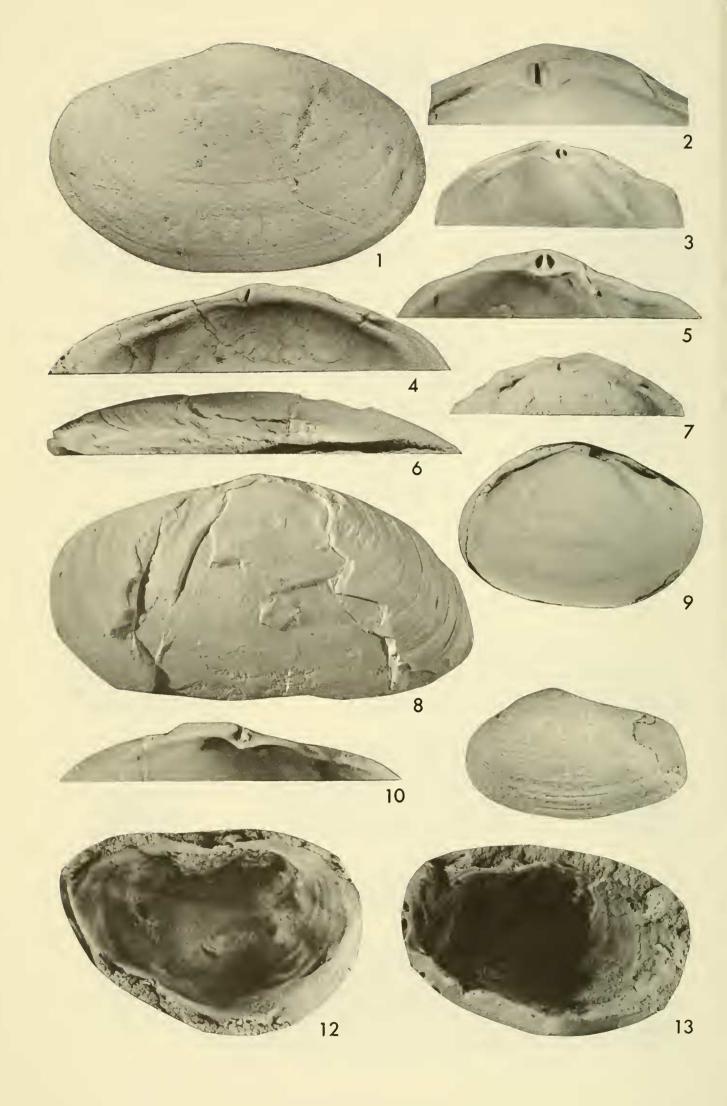
Fig. 2. Protodonax? sp. indet.

2. YPM 24473, A950, Loc. 97, Colgate lithofacies, ILM. ×2.

Fig. 3-15. Tellinimera scitula (Meek & Hayden)

- 3. YPM 24460, A1209, Loc. 136, LEl, TCM, Upper nicolleti AZ; showing a very strongly projecting ligament. ×2.
- 4. YPM 24458, A1311, Loc. 178, TLM; a steinkern showing faintly impressed pallial line and sinus. ×2.
- 5. YPM 24455, A476, Loc. 212, ICl, TCM, Cymbophora-Tellinimera AZ; showing ligament retained on the nymphs and the posteroventral twist of the valves. ×3.
- 6. YPM 24454, A747, Loc. 226, TLM, Cucullaea AZ. ×3.
- 7, 9. YPM 24501, A462, Loc. 210, ICl, TCM, Cymbophora-Tellinimera AZ; notice pallial sinus on figure 7. Fig. 7 ×3; fig. 9 ×6.
- 8. YPM 24461, A1192, Loc. 130, ICl, TCM, Cymbophora-Tellinimera AZ; with projecting ligament. ×2.
 10, 12, 13. YPM 24456, A462, Loc. 210, ICl, TCM, Cymbophora-Tellinimera AZ; showing
- 10, 12, 13. YPM 24456, A462, Loc. 210, ICl, TCM, Cymbophora-Tellinimera AZ; showing hinges (teeth incomplete), nymph, pallial sinus and striae on the inner surface of the shell. Fig. 10 ×3; figs. 12, 13 ×6.
- 11. YPM 24459, A1209, Loc. 137, LEI, TCM, Upper nicolleti AZ. ×2.
- 14. YPM 24458, A1311, Loc. 178, TLM, hinge of a left valve. ×4.
- 15. YPM 24452, A471, Loc. 211, ICl, TCM, Cymbophora-Tellinimera AZ; a ventral view of hinge, showing the bifid cardinal teeth and small muscle scar insertion pits. ×4.5.





Figs. 1–10. Sourimis equilateralis (Meek & Hayden)

- 1. GCS type No. 20195, GCS Loc. 23726, Halfbreed Creek, Alberta, Pakowki Formation, Bear Gulch Sandstone Lentil, R. W. Landes, Collector. ×2.
- 2. YPM 24467, A645, Loc. 70, LEI, TCM, Protocardia-Oxytoma AZ; rubber latex cast of right valve hinge. ×2.
- 3. YPM 24463, A1047, Loc. 238, LEI, TCM, Lower nicolleti AZ; rubber latex cast of the interior of a left valve, showing the strong anterior and weak posterior buttresses. ×1.
- 4. GCS type No. 20197, GCS Loc. 23732, Bear Gulch, Alberta, Pakowki Formation, Bear Gulch Sandstone Lentil, R. W. Landes, Collector; right valve hinge. ×2.
- 5. YPM 24466, A560, Loc. 191, LEl, TCM, Lower nicolleti AZ; latex cast of left valve hinge. ×2.
- 6, 8. USNM 179, "Mouth of Judith River, Montana", Judith River Formation, Upper Campanian; the original of Plate 39, fig. 5a of Meek (1876); figure 6 shows the depressed anterodorsal margin of the left valve. ×2.
- 7. YPM 24465, A362, Loc. 46, LEI, TCM, Lower *nicolleti* AZ; latex cast of right valve hinge. ×1.
- 9. YPM 24462, A734, Loc. 86, LEl, TCM, Protocardia-Oxytoma AZ; a steinkern showing shape, adductor muscle insertion areas, and pallial line. ×1.
- 10. YPM 24468, A399, Loc. 51, LEI, TCM, Lower *nicolleti* AZ; a rubber latex cast of left valve hinge. ×2.

Figs. 11-13. Hiatella? sp. A

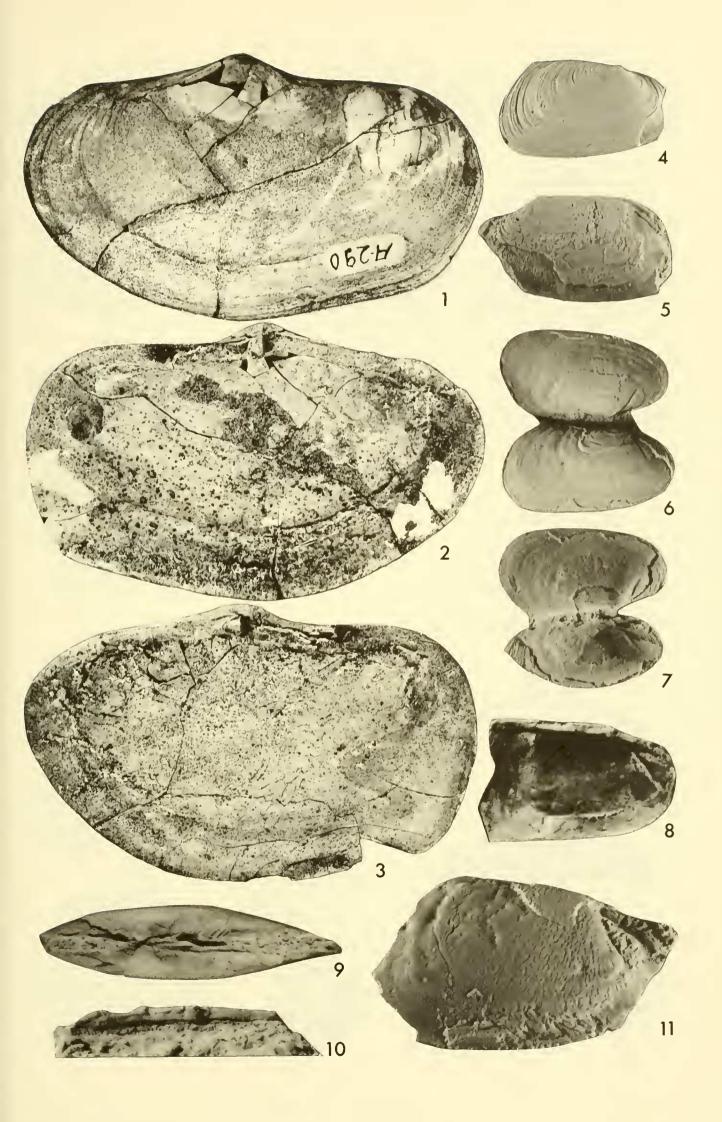
- 11. YPM 24471, A959, Loc. 104. ×2.
- 12. YPM 24472, A1073, Loc. 243; rubber latex cast of a left valve showing small resilifer pit and nymph. ×6.
- 13. YPM 24470, A529, Loc. 218; rubber latex cast showing hinge of right valve. ×6. All from LEI, TCM, Lower *nicolleti* AZ.

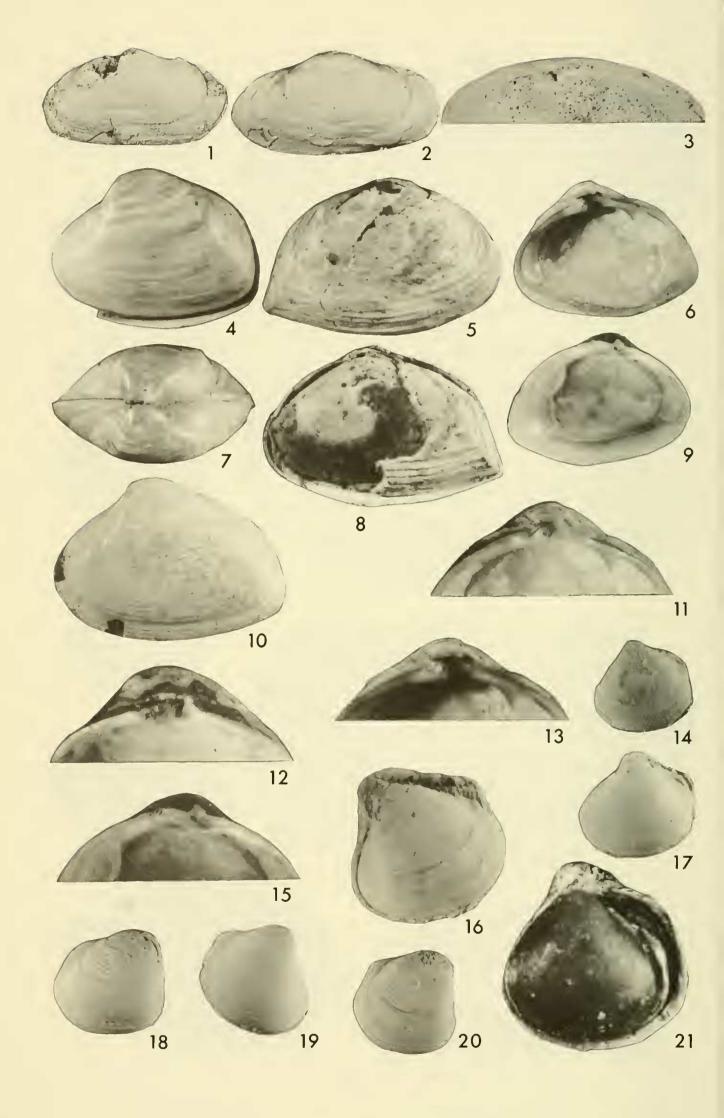
Figs. 1-3. Panopea occidentalis Meek & Hayden

YPM 24469, A290, Loc. 207, TLM, Tancredia-Ophiomorpha Biofacies; showing hinges, 1-3. pallial line and adductor insertion areas. $\times 1$.

Figs. 4-11. Cyrtodaria minuta Speden, sp. n.

- YPM 24484, A476, Loc. 212, ICl, TCM, Cymbophora-Tellinimera AZ. ×6.
- 5, 11. YPM 24486, A441, Loc. 56, ICl, TCM, Cymbophora-Tellinimera AZ; Fig. 11 shows adductor muscle insertions. Fig. 5 ×4; fig. 11 ×6.
 YPM 24481, A1204, Loc. 132, ICl, TCM, Cymbophora-Tellinimera AZ; holotype,
- showing steinkerns and matching shell interiors. ×4.
- YPM 24482, A612, Loc. 220, LEI, TCM, Lower nicolleti AZ; rubber latex cast showing 8.
- the hinge of a left valve and the strong anterior buttress ridge. ×9. YPM 24485, A532, Loc. 218, LEl, TCM, Lower nicolleti AZ; dorsal view showing 9. nymph. $\times 12$.
- YPM 24483, Loc. 212, ICl, TCM, Cymbophora-Tellinimera AZ; right valve hinge and 10. nymph (center of hinge later destroyed). $\times 6$.





Figs. 1-3. *Mya*? sp. A

1, 3. YPM 24494; a shell, and rubber latex cast of left valve showing chrondophore.

Fig. 1 \times 1; fig. 3 \times 1.5.

2. YPM 24493; rubber latex cast. $\times 1$.

Both specimens from A256, Loc. 16, Colgate lithofacies, ILM.

Figs. 4-13, 15. Varicorbula crassimarginata (Meek)

4, 7. YPM 24497, A459, Loc. 210, ICl, TCM, Cucullaea AZ; showing the ventral and posterodorsal overlap of the larger right valve. ×6.

5, 8. YPM 24496, A1180, Loc. 121, LEI, TCM, Protocardia-Oxytoma AZ; an abnormal specimen with a sharp umbonal to posteroventral margin keel. ×6.

6, 9, 11–13, 15. YPM 24495, A460, Loc. 210, ICI, TCM; interiors showing hinges, pallial line and sinus, and adductor muscle insertion areas. Figs. 6, 9 ×6; figs. 11–13, 15 ×9.

10. YPM 24498, A654, Loc. 73, ICl, TCM, Cucullaea AZ. ×6.

Figs. 14, 16-21. Corbulamella gregaria (Meek & Hayden)

14. YPM 24164, A305, Loc. 26. ×8. 16, 20. YPM 24160. Fig. 16 ×12; fig. 20 ×8.

17, 19. YPM 24161. ×8. 18. YPM 24162. ×8.

All from one assemblage, A1306, Loc. 177, showing the inequivalveness and variation of the ornament (especially on the left valve).

21. YPM 24167, A1304, Loc. 177; showing the smaller left valve. $\times 12$.

All specimens from LEI, TCM, Limopsis-Pseudoptera AZ.

Figs. 1-6. Corbulamella gregaria (Meek & Hayden)

- 1. YPM 24158, A1306, Loc. 177, a block showing the typical clustered mode of occurrence. ×1.
- 2. YPM 24166, A561, Loc. 191; lamella incomplete. ×24.
- 3, 4. YPM 24163, A301, Loc. 26; showing the hinge and the lamella which bears the posterior adductor muscle insertion. ×24.
- 5. YPM 24157, A561, Loc. 191; showing posterior lamella. ×24.
- 6. YPM 24168, A1034, Loc. 177; showing the lamellae and the interlocking of the chondrophore and tooth. ×18.

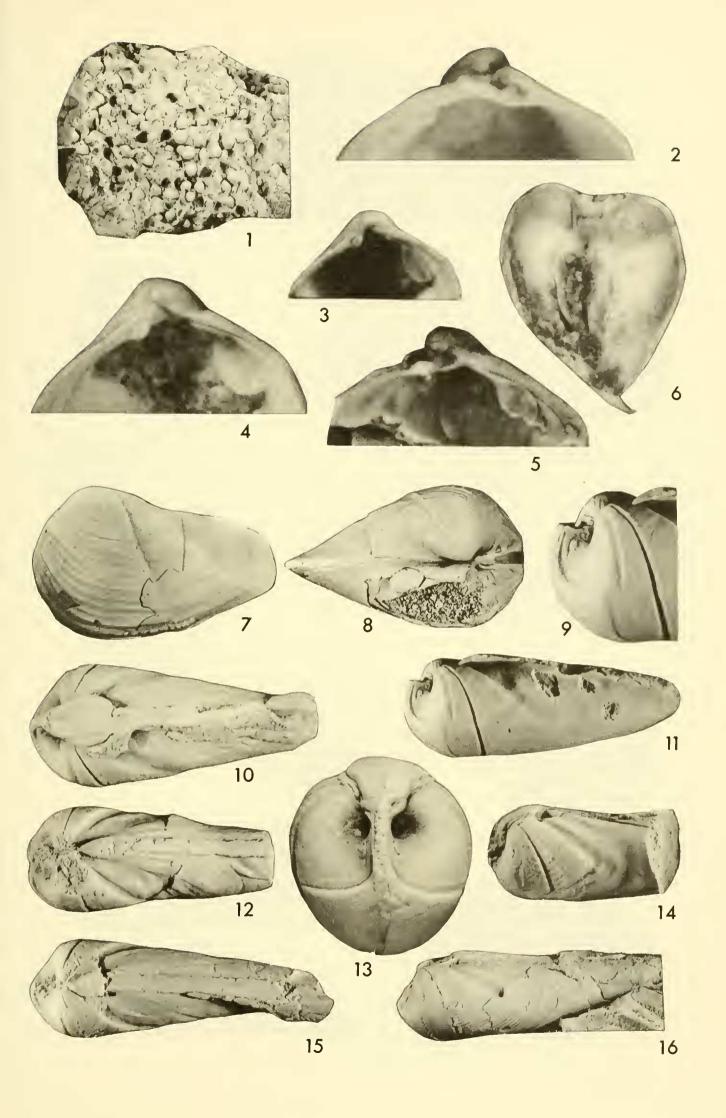
All from LEI, TCM, Limopsis-Pseudoptera AZ.

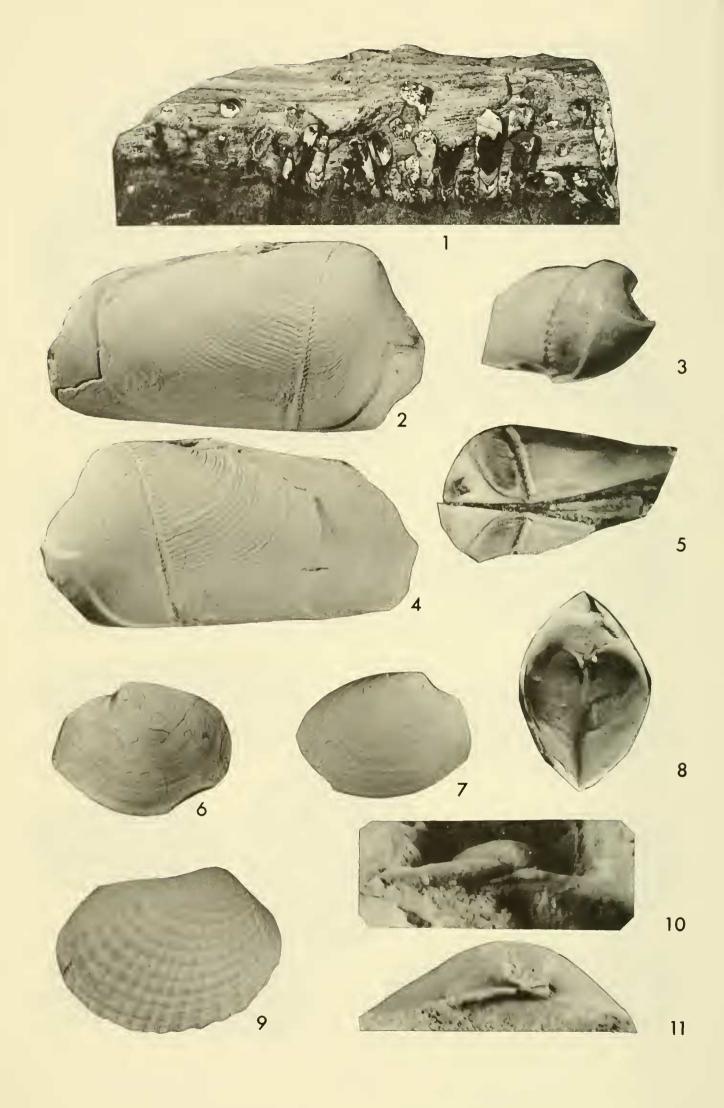
Figs. 7-8. Parapholas sp. A

7, 8. YPM 24492, A653, Loc. 73, ICl, TCM, Cucullaea AZ. ×1.

Figs. 9-16. Opertochasma cuneatum (Meek & Hayden)

- 9, 11. YPM 24480; showing the accessory adductor, anterior adductor and posterior adductor muscle insertion areas. Fig. 9 ×6; fig. 11 ×4.
- 10, 13. YPM 24490; showing the mesoplax, and the row of discontinuous pallial insertion areas above the callum. Fig. 10 ×6; fig. 13 ×9.
- 12. YPM 24499; showing the rodlike apophysis in the umbone of the left valve. ×6. Figs. 9–13 from A943, Loc. 95, LEI, TCM, Lower *nicolleti* AZ.
- 14. YPM 24479, A723, Loc. 82, LEI, TCM, Upper nicolleti AZ; showing mesoplax and posterior adductor insertion. ×4.
- 15. YPM 24491, A943, Loc. 95, LEI, TCM, Lower *nicolleti* AZ; showing ornament on the impression of the basal surface of the mesoplax, and the impression of the metaplax. ×4.
- 16. YPM 24489, A723, Loc. 82, LEI, TCM, Upper nicolleti AZ. ×2.





Figs. 1-5. Opertochasma cuneatum (Meek & Hayden)

- 1. YPM 24488, A943, Loc. 95, LEl, TCM, Lower nicolleti AZ; a block showing the radial orientation of specimens in a large fossilized wood fragment. ×1.
- 2, 4. ANSP 16286, Mingusville, Montana, Pierre Shale, Homer Squyer, Collector; specimen showing ornament. ×4.
- 3. YPM 24478; showing the discontinuous pallial line along the margin of the callum. ×6.
- 5. YPM 24479; showing the central adductor insertion area, the condyle, and the row of discrete pallial insertion areas along the margin of the callum plate. ×6. Figs. 3 and 5 from A723, Loc. 82, LEl, TCM, Upper nicolleti AZ.

Figs. 6-8. Periploma subgracile (Whitfield)

- 6. YPM 24156, A454, Loc. 210, ICl, TCM, Cymbophora-Tellinimera AZ; a steinkern with some shell remaining anteriorly, and showing the pallial sinus and posterior adductor muscle insertion area. ×1.
- 7. YPM 24154, A478, Loc. 212, ICl, TCM, Cymbophora-Tellinimera AZ. ×2.
- 8. YPM 24155, A1099, Loc. 248, LEl, TCM, Lower nicolleti AZ; a rubber latex cast showing an internal view of the hinge. ×2.

Figs. 9-11. Pholadomya deweyensis Speden, sp. n.

- 9. YPM 24152, A1227, Loc. 145, LEI, TCM, Protocardia-Oxytoma AZ; holotype. ×1.5.
- 10. YPM 24151, A1168, Loc. 110, LEI, TCM, Lower nicolleti AZ; a rubber latex cast of a left valve hinge. ×12.
- 11. YPM 24153, A546, Loc. 219, LEl, TCM, Lower nicolleti AZ; a dorsal view of a left valve to show the nymph. ×12.

Figs. 1-7. Goniomya americana Meek & Hayden

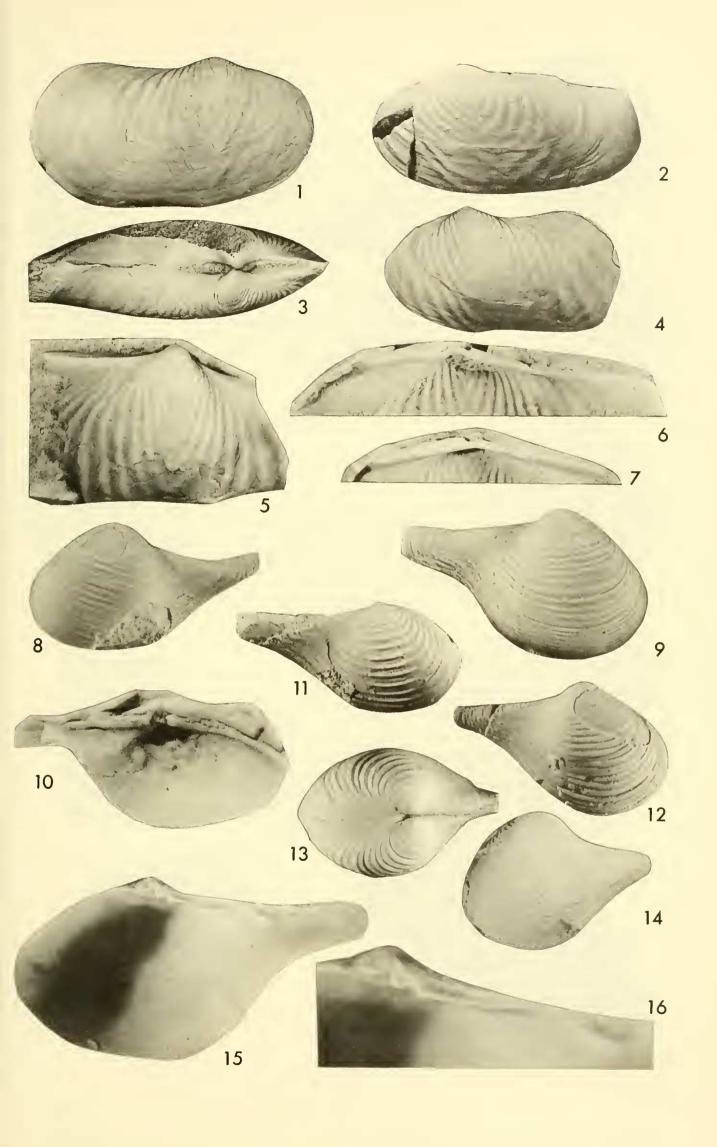
- 1. YPM 24150. ×1.
- 2. YPM 24149. ×1.
- 3. YPM 24147. ×1. All from A345, Loc. 35, TLM, Cucullaea AZ.
- 4. YPM 24148, A740, Loc. 87, TLM. ×1.
- 5. YPM 24145, A1106, Loc. 249, LEI, TCM, Lower nicolleti AZ; a rubber latex cast. ×2.
- 6. YPM 24146, A1012, Loc. 234, LEI, TCM, Lower nicolleti AZ; a rubber latex cast showing edentulous hinge and strong nymph. ×2.
- 7. YPM 24145, A1106, Loc. 249, LEI, TCM, Lower nicolleti AZ; rubber latex cast showing hinge and nymph. ×2.

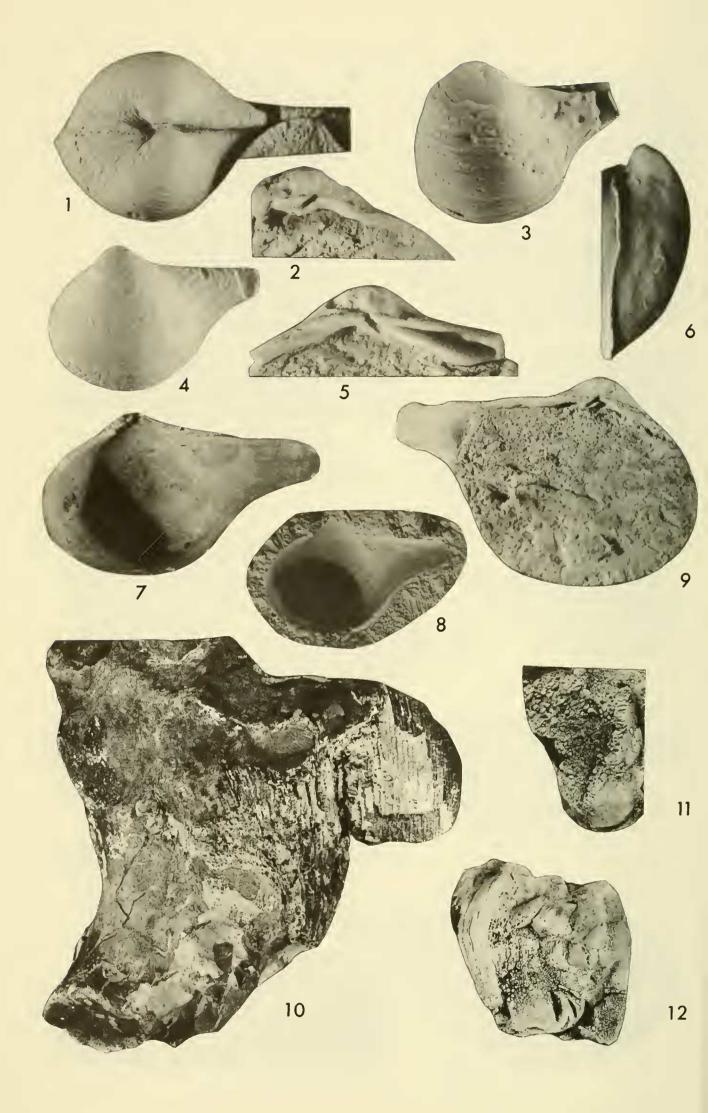
Figs. 8-16. Cuspidaria moreauensis (Meek & Hayden)

- 8. YPM 24136, A244, Loc. 11. ×6.
- 9. YPM 24134, A590, Loc. 66. ×6.
- 10. YPM 24132, A1099, Loc. 248; interior of dorsal margin showing the deep pedal muscle insertion area. ×9.
- insertion area. ×9.

 YPM 24144, A704, Loc. 206; showing the two radial costae on the dorsal surface of the rostrum. ×9.
- 12. YPM 24135, A1244, Loc. 150, LEI, TCM, Upper nicolleti AZ. ×6.
- 13. YPM 24131, A1099, Loc. 248; a dorsal view showing the anterodorsal margin of the left valve overlapping that of the right valve. ×9.
- 14. YPM 24133, A623, Loc. 222, a specimen with a short rostrum, ×6.
- 15-16. YPM 24500, A1209, Loc. 136, LEI, TCM, Upper nicolleti AZ; a rubber latex cast of hinge showing ligament pit, the posterior lamella, and the linear ridge behind the posterior adductor insertion area. Fig. 15 ×9; fig. 16 ×18.

 All except figs. 12, 15, 16 from LEI, TCM, Lower nicolleti AZ.





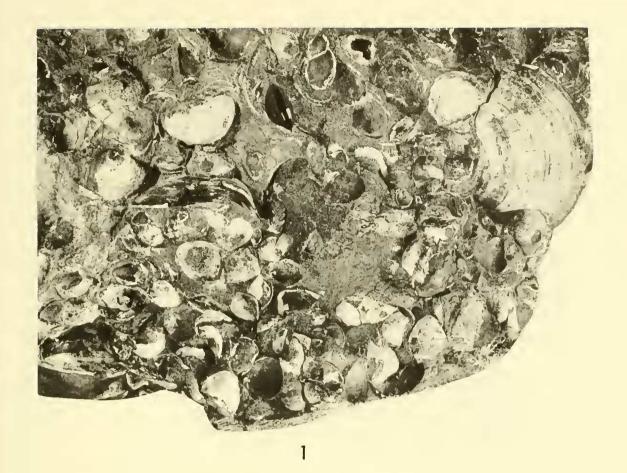
Figs. 1-9. Cuspidaria ventricosa (Meek & Hayden)

- 1. YPM 24142, A1245, Loc. 150, LEI, TCM, Upper *nicolleti* AZ; showing only one weak costa on the posterodorsal surface. ×6.
- 2. YPM 24138, A797, Loc. 92, ICl, TCM, Cucullaea AZ; a left valve hinge. ×12.
- 3. YPM 24141, A974, Loc. 100, ICl, TCM, Cucullaea AZ. ×4.
- 4. YPM 24143, A1120, Loc. 228, LEI, TCM, Limopsis-Pseudoptera AZ. ×8.
- 5. YPM 24139, A920, Loc. 92, ICl, TLM, Cucullaea AZ; a right valve hinge. ×12.
- 6. YPM 24745, A1180, Loc. 121, LEI, TCM, Protocardia-Oxytoma AZ; a steinkern showing pedal muscle insertions. ×9.
- 7-8. YPM 24140, A465, Loc. 210, ICl, TCM, Cucullaea AZ; interior of a right valve, taken with different lighting, to show posterior adductor insertion area, the weak ridge behind the adductor area, and the overlap of the ventral margin of the left valve. Fig. 7 ×6; fig. 8 ×4.
- 9. YPM 24137, A799, Loc. 92, ICl, TCM, Cucullaea AZ; a left valve hinge. ×6.

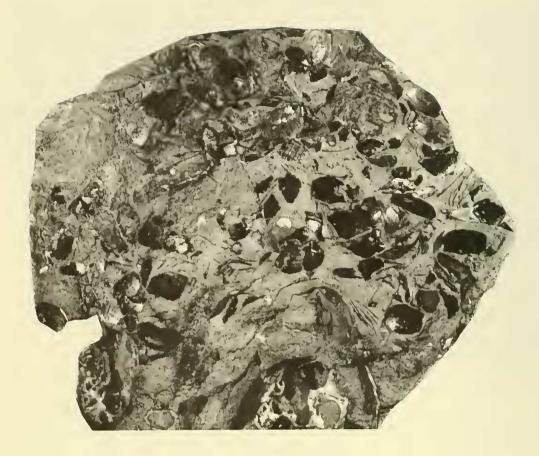
Figs. 10-12. Ichthyosarcolites? sp. A

- 10. YPM 24697, A944, Loc. 95; a specimen showing the shape and one of the projecting flanges. ×1.
- 11-12. YPM 24696, A604, Loc. 66; fragments showing the cellular structure of the outer wall (fig. 11) and the septate basal portion of the body chamber (fig. 12). ×1. All from the LEI, TCM, Protocardia-Oxytoma AZ.

- Fig. 1. YPM 24740, A1269, Loc. 164, TLM, Cucullaea AZ. A block showing a Protocardia-Cymbophora association. The large shells are Cymbophora, and the small numerous specimens are Protocardia. Rare gastropods are also visible. Note the hollow specimens partially filled with calcite crystals. ×1.
- Fig. 2. YPM 24739, A657, Loc. 73, ICl, TCM, Cucullaea AZ. A block showing a Cucullaea association. ×1.









- Fig. 1. YPM 24738, A518, Loc. 216, LEl, TCM, Lower nicolleti AZ. A block with a concentration of fish scales and rare bones, and with scattered molluscs including ammonoids. ×1.
- Fig. 2. YPM 24400, A981, Loc. 102, LEI, TCM, Protocardia-Oxytoma AZ. A block showing a Protobranch Association. Numerous specimens of Nuculana scitula, and common ones of Malletia evansi, mixed with abundant light- and dark-colored plant fragments. ×1.